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TABLE OF CONTENTS

MacCALL, A. D.
1986. Virtual population analysis (VPA) equations for nonhomogeneous populations, and a family of approximations including improvements on Pope's cohort analysis. Can. J. Fish. Aquat. Sci. 43(12):2406-2409. 8659

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TABLE OF CONTENTS (CONTINUED)

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UCHIDA, RICHARD N.
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TABLE OF CONTENTS (CONTINUED)

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TABLE OF CONTENTS (CONTINUED)

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8659

Virtual Population Analysis (VPA) Equations for Nonhomogeneous Populations, and a Family of Approximations Including Improvements on Pope's Cohort Analysis

Alec D. MacCall

Southwest Fisheries Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038, USA

MacCall, A. D. 1986. Virtual population analysis (VPA) equations for nonhomogeneous populations, and a family of approximations including improvements on Pope's cohort analysis. Can. J. Fish. Aquat. Sci. 43: 2406–2409.

A set of "backward" virtual population analysis (VPA) equations relates catch (C_t) from continuous fishing between times t and $t + 1$ to population size (N_t, N_{t+1}) when a portion of the stock is unavailable to fishing. The usual VPA equations become a special case where the entire stock is available (i.e. the stock is homogeneous). A close approximation to the VPA equations is $N_t = N_{t+1} \exp(M) + C_t M/(1 - \exp(-M))$, which has properties similar to Pope's "cohort analysis" and is somewhat more accurate in the case of a continuous fishery, especially if the natural mortality rate (M) is large. Much closer simple approximations are possible if the seasonal pattern of catches is known.

Une série d'équations d'analyse de population virtuelle (APV) « à rebours » lie les prises (C_t) tirées de la pêche continue entre les temps t et $t + 1$ à la taille de la population (N_t, N_{t+1}) quand une partie du stock n'est pas disponible pour la pêche. Les équations habituelles d'APV deviennent un cas spécial là où le stock en entier est disponible (c.-à-d. que le stock est homogène). Une approximation étroite des équations d'APV est $N_t = N_{t+1} \exp(M) + C_t M/(1 - \exp(-M))$ qui a des propriétés semblables à l'analyse par cohortes de Pope et est un peu plus précise dans le cas d'une pêche continue, surtout si le taux de mortalité naturelle (M) est important. Des approximations simples beaucoup plus étroites sont possibles si l'on connaît la tendance saisonnière des prises.

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Virtual population analysis (VPA), also known generically as cohort analysis, has come to be the preeminent method of fish stock assessment since its appearance 20 yr ago (Gulland 1965; Murphy 1965). The method usually is used in the form of a "backwards solution" where historical abundances of a cohort are estimated on the basis of subsequent catches from a presumed homogeneous stock: all fish of a specified age are assumed to be equally susceptible to capture. The equations unfortunately do not allow convenient separation of the unknown quantities from the known and/or assumed quantities, so the solution must be obtained by numerical methods, e.g. Sims (1982), or by approximation, e.g. Pope's (1972) popular "cohort analysis." Computers have made numerical solution very easy, but there remain applications of approximation methods. For example, Pope's approximation has proved useful for statistical and mathematical analysis of the behavior of VPA, whereas the exact equations are intractable. In practice, good approximations and efficient algorithms remain useful, as computers may not conveniently be available in working group meetings, in field locations, and in some developing countries.

The following discussion provides two extensions to existing VPA methods. The first is a set of equations which include possible assumptions concerning homogeneity of cohorts, i.e. part of the cohort may not be available or vulnerable to fishing. These equations also provide the basis for an easy and rapid iterative backward solution of the VPA equations. The second is description of a family of approximation formulas which are similar in concept to Pope's cohort analysis.

VPA Equations for Nonhomogeneous Populations

Assume that the cohort consists of two segments, one fished and one unfished (cf. Widrig 1954). This division could arise under a variety of circumstances. For example, some members of the cohort may reside in habitats or regions which cannot be fished. Another possibility is differential vulnerability to the gear, depending on fish size or other attribute. The present treatment corresponds to the common model of "knife-edge" gear selection. Importantly, there must be no interchange between the two segments during the time interval. Let P be the age-specific fraction of the cohort which is subject to fishing at the beginning of a time interval. The remaining notation follows that of Ricker (1975), except that F refers to the instantaneous coefficient of fishing mortality *on the fishable segment of the cohort*. As usual, F and M are assumed to be independent, and M has the same value in both segments. Both of these assumptions are open to question (e.g. Lawless 1982, p. 491; Ricker 1976), but there seems to be no practical alternative given the usual state of knowledge. All parameters are assumed to be constant within the time period, but may vary among ages or time periods. A full notation is useful for fishery analysis, but requires extensive use of subscripts denoting age and time; this notation can be developed by the reader for particular applications (Schnute 1985 provides a useful structure for this purpose). The present notation is simplified for ease of exposition, and considers a single cohort and a unit time period. The time subscript t is shown only where desirable for clarity. Under continuous fishing, the catch (C_t) for a unit time period beginning at time t, and ending at time $t + 1$, is given by

(1) $C_t = N_t PFA/Z$

where $Z = F + M$, and $A = 1 - \exp(-Z)$. The abundance at the beginning of the next time period is

(2) $N_{t+1} = N_t P\exp(-Z) + N_t(1-P)\exp(-M)$

where the two additive terms on the right side represent contributions from the fished and the unfished segments, respectively. This expression may be rearranged to give

(3) $N_{t+1} = N_t P\,[\exp(-Z) - \exp(-M)] + N_t\exp(-M)$

and equation (1) allows substitution of $C_t Z/FA = N_t P$, giving

(4) $N_{t+1} = (N_t - C_t mZ/FA)\exp(-M)$

where $m = 1 - \exp(-F)$. The backward solution therefore is

(5) $N_t = N_{t+1}\exp(M) + C_t mZ/FA.$

Equations (4) and (5) also can be derived from the equations describing the usually assumed homogeneous case. However, because P appears in equations (1) and (2), but not in (4) or (5), this derivation demonstrates that they have the somewhat surprising property of being true whether or not the homogeneity assumption ($P = 1$) is met, *provided that F is defined appropriately*. These equations also demonstrate that for a given catch and natural mortality rate, the four variables, N_t, N_{t+1}, P, and F, possess only two degrees of freedom among them. This means that specification of any two values should determine both remaining values, but this property may be of limited use as the basis for direct parameter estimation (e.g. for a given catch, F and P covary strongly, and estimation errors could easily lead to misinterpretation). In practice, one value is given; for example, in the case of a backwards solution, N_{t+1} may have been provided by an initial guess or by VPA of older aged catches. The second value is imposed by a simultaneous equation which may explicitly or implicitly fix P (see equations (6) and (7), respectively). Equation (5) is aesthetically attractive in that it clearly expresses the sense of "virtual population" as a modified sum of subsequent catches.

There are many possible equations which give F as a function of P, N_t, N_{t+1}, and M, depending on the assumed behavior and distribution of the stock and fishery. Differences among these equations become especially important when they are applied sequentially to link successive ages, as is the usual case in VPA. For example, equation (2) can be rearranged algebraically to give

(6) $F = -\ln\left[\dfrac{(P-1)N_t + N_{t+1}\exp(M)}{PN_t}\right]$

However, if P is treated as an independent population parameter, sequential use of this equation must be based on an assumed redistribution of all of the survivors at the end of each time period, so that the individuals in the fished and unfished segments have no differential tendency to remain in their previous states. Alternatively, if P can be estimated independently for individual ages and times, perhaps from surveys of habitat distribution or of size composition, equation (6) allows exploitation rates to be separated into component sources of variation: those associated with changes in P and those associated with changes in F on the available segment. This form of "separable VPA" (sensu Doubleday 1976) is being developed by Daniel Kimura (NMFS-NWAFC, BIN C15700, 7600 Sandpoint Way N.E., Seattle, WA 98115, USA, manuscript in revision). Of course, in the case of homogeneity ($P = 1$), equation (6) simplifies to

(7) $F = \ln(N_t/N_{t+1}) - M$

as was suggested by Pope (1972).

Equations (5) and (7) also provide a convenient rapid algorithm for solving the usual VPA equations for a homogeneous stock. The procedure is as follows: (1) given C_t, N_{t+1}, and M, use Pope's approximation or the improved approximation described below to obtain a first estimate of N_t; (2) use this value of N_t in equation (7) to obtain an estimate of F; (3) use this value of F in equation (5) to get an improved estimate of N_t; (4) repeat steps 2 and 3 until the desired level of precision is reached, judging by the change from the estimate in the previous iteration; and (5) repeat the procedure on the next younger age of the cohort, letting the previous N_t now be N_{t+1}, and go to step 1. The rate of convergence is very high (Fig. 1), approaching that of Newton's method as described by Sims (1982); two iterations often are sufficient. Also, this method does not converge to extraneous solutions.

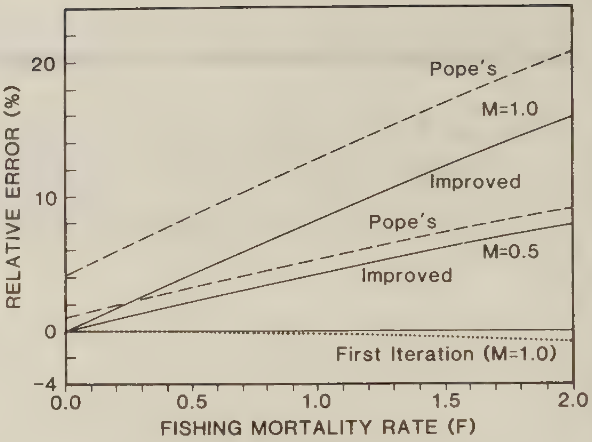

FIG. 1. Relative error (see text for definition) of Pope's and the new approximation for a homogeneous stock ($P = 1$) and two values of M. For comparison, the relative error of the result of the first iteration of the VPA algorithm is shown for $M = 1$, where relative error is defined as $((\hat{m}\hat{Z}/\hat{F}\hat{A})/(mZ/FA)) - 1$.

A Family of Approximations

The independence of C_t in equation (5) indicates that there exists a family of VPA approximations of the form

(8) $\hat{N}_t = N_{t+1}\exp(M) + C_t V(F,M,\ldots)$

where $\hat{N}_t$ is an approximation of N_t and $V(F,M,\ldots)$ is a function approximating the value of mZ/FA. These approximations are applicable to nonhomogeneous fisheries ($P \neq 1$) as well as the more commonly assumed homogeneous fisheries. In the case of nonhomogeneous fisheries, these equations need to be coupled with an equation such as (6).

Pope's (1972) cohort analysis is a member of this family of approximations, where $V = \exp(M/2)$:

$$(9) \quad \hat{N}_t = N_{t+1}\exp(M) + C_t\exp(M/2).$$

Another approximation is provided by a first-order Taylor series approximation of the exponentials in the left side of the expression

$$(10) \quad mn/A \approx FM/Z$$

where $n = 1-\exp(-M)$. Rearrangement of (10) gives

$$(11) \quad V = mZ/FA \approx Mn$$

which may be substituted into equation (8) to give

$$(12) \quad \hat{N}_t = N_{t+1}\exp(M) + C_tM/n.$$

The relative accuracy of approximations (9) and (12) can be expressed as the relative error in V, the coefficient of C_t; the remaining terms of the equations are identical and tend to reduce clarity of the comparisons. Also, because equations (9) and (12) are linear in C, errors in the coefficients propagate in a straightforward manner. Let the "relative error" (r_x) of an approximation, $\hat{X}$, be defined as $r_x = (\hat{X} - X)/X$, or equivalently, $r_x = (\hat{X}/X)-1$, where X is the true value. In the present case, the approximation is the coefficient applied to C_t in equations (9) and (12), and the true value is the coefficient mZ/FA in equation (5)). Thus, the relative error for Pope's approximation ($r_{(11)}$) is

$$(13) \quad r_{(9)} = \frac{\exp(M/2)}{mZ/FA} - 1$$

where $\exp(M/2)$ is Pope's cohort analysis coefficient of C_t. Similarly, the relative error of the new approximation in equation (12) is

$$(14) \quad r_{(12)} = \frac{M/n}{mZ/FA} - 1.$$

Relative errors for these two approximations are compared in Fig. 1; generally, the differences are not large. The relative error of the new approximation in equation (12) is slightly but consistently smaller than that of Pope's approximation. The new approximation becomes considerably better than Pope's as M becomes large, thus extending the range of mortality rates under which approximation is useful. Taylor series expansions of the relative errors, equations (13) and (14), clarify the nature of the difference between the two approximations. If we discard terms higher than quadratic, the relative error for Pope's approximation is $(2FM + M^2)/24$, whereas that of the new approximation is $(2FM)/24$. The constant factor of $M^2/24$ in Pope's relative error explains both its nonzero intercept at $F = 0$ and the parallel appearance of the plots in Fig. 1.

Pope's approximation is equivalent to assuming that the entire catch is taken instantaneously at midyear. The new approximation does not have a corresponding convenient interpretation. A tentative interpretation may be derived from the relationship $\bar{N} = N_0n/M$, which describes average abundance ($\bar{N}$) over a unit time interval versus initial abundance (N_0), if only natural mortality is acting. Thus, the quantity M/n used in the new approximation is equal to $N_0/\bar{N}$ if there is only natural mortality. Paradoxically, this means that the new approximation assumes the fishery's catch to be a continuous sampling of natural deaths in the absence of a fishery. This somewhat strange interpretation is consistent with the fact that the new approximation is identical to the expression which results from taking the limit of equation (5) for a given catch as $F \rightarrow 0$.

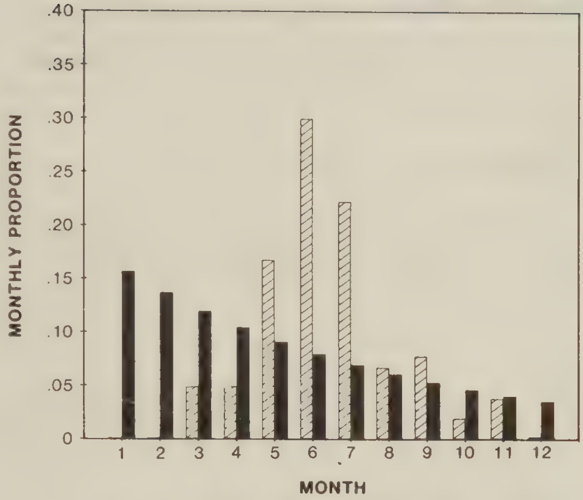

FIG. 2. Comparison of monthly catch distribution under the assumption of constant F and that from a seasonal fishery (the California catch of mackerel in 1941–42, Anonymous 1944).

VPA Approximation for Seasonal Fisheries

The usual assumption in VPA is that F is constant over the time interval under consideration. This assumption requires that the catch decline exponentially over that interval. Many, if not most, fisheries are seasonal, so the pattern of catches over the year or season does not conform to this assumption (Fig. 2). A standard practice in these cases is to divide the fishing year into shorter time periods such as quarters or months, within which F is more nearly constant.

If the seasonality of the fishery is predictable, a useful approximation can be developed as follows. If the exact time (t_i) of each catch (C_t) were known, VPA equation (8) would reduce to

$$(15) \quad N_t = N_{t+1}\exp(M) + \sum_i C_t\exp((t_i - t_0)M)$$

where t_0 is the beginning of the fishing year. Equivalently, if the proportion (p_i) of the total catch (C_t) taken at time t_i is known, we have

$$(16) \quad N_t = N_{t+1}\exp(M) + C_t\sum_i p_i\exp((t_i - t_0)M).$$

Equation (16) has the same form as equation (8), demonstrating that seasonal fisheries can be treated by the same family of approximations. Moreover, equation (16) requires information only on M and the temporal distribution of catches, making function V_{seas}, and hence the VPA, independent of estimated F.

In practice, the value of V_{seas} for a seasonal fishery can be obtained from sequential VPA of the typical monthly proportions of the total annual catch (see example below). By setting N_{t+1} to zero, V_{seas} is given directly by the virtual population of the p_i values at time t_0, this being equivalent to the summation in equation (16).

Application of Approximations

Parrish and MacCall (1978) gave VPA estimates for mackerel (*Scomber japonicus*), based on annual catch-at-age data, $M = 0.5$, and assumed constant F within the fishing season. Estimated F for fish aged 4 and older in the 1941−42 fishing year (May through April) was 1.115, giving a V_{annual} of $mZ/FA = 1.2152$. The monthly proportions of the total unaged annual catch are based on Anonymous (1944) and are shown in Fig. 2. These monthly catches are in weight rather than numbers, causing some error due to individual growth during the year. A value of V_{seas} can be approximated by letting $V_{month} = (M/12)/(1-\exp(-M/12))$. The annual value of V based on the seasonal catch distribution is approximately

$$(17) \quad V_{seas} = \sum_{i=1}^{12} p_i V_{month} \exp((i-1)M/12)$$

giving $V_{seas} = 1.2851$. Thus, the relative error of Parrish and MacCall's annually based VPA is approximately −5.4% for this year, indicating a moderate underestimate of abundance, given the assumptions. Interestingly, the new VPA approximation in equation (12) gives $V_{new} = 1.2707$, and Pope's approximation gives a nearly exact value of $V_{Pope} = 1.2840$. Pope's approximation does well because in this case the actual catch was indeed taken very near midyear. Of course, other seasonal distributions may produce values of V_{seas} ranging from 1.0 (all the catch taken at year's end) to $\exp(M)$ if all of the catch is taken at the beginning of the year.

Differences in VPA estimates of abundance due to various homogeneity assumptions and/or approximations often fall within the variability due to imprecision in the value of the natural mortality rate, M. For example, given $M = 0.5$ and constant $F = 0.5$, Pope's approximation using $M = 0.48$ would have the same relative error as the new approximation using $M = 0.5$. The difference becomes larger for large M: given $M = 1.0$ and constant $F = 1.0$, Pope's approximation would require $M = 0.92$ to produce a relative error equal to that of the new approximation. Violations of the assumption of constant F over the time period can produce somewhat larger errors. The relative error of Parrish and MacCall's annual VPA in the preceding example is roughly equal to the relative error which would have occurred if they had used a seasonally corrected VPA with $M = 0.39$, which is 22% smaller than assumed M.

It can be argued that the choice of approximations is inconsequential because imprecision associated with alternative VPA approximations and assumptions is smaller than that associated with imprecision in assumed M. A counterargument is that errors due to approximations or assumptions are systematic biases and should be recognized as such. If a value of M is stated, VPA using that M should as nearly as possible reflect that value, rather than some systematically different effective value arising from the properties of an unnecessary assumption or approximation.

Acknowledgements

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Alec D. MacCall

4. Changes in the Biomass of the California Current Ecosystem

ABSTRACT

California Current pelagic fishes have been monitored for 30 to 50 years, and a paleosedimentary record extends back 200 to 2000 years. Large natural fluctuations in abundance occur at all time scales. Overharvest of sardines removed a major component of the ecosystem; the extent to which it was replaced by other species (e.g., anchovy, rockfish) is not clear. Large predatory fishes have declined in abundance due to exploitation. Pinnipeds were depleted in the last century, but now are abundant and are increasing rapidly. Seabird reproductive success is closely related to availability of small forage fish such as anchovy. Despite a wealth of scientific information, species interactions are poorly understood, and are difficult to separate from independent differential responses to varying environmental conditions. The biological basis of fishery management is likely to remain single-species models in the foreseeable future. Ecosystem management requires coordinated consideration of both fished and non-fished species, but faces conflicting jurisdictions and other institutional difficulties.

INTRODUCTION

The California Current sweeps southward along the west coast of North America, with its main influence extending from about the Columbia River to central Baja California (Figure 4.1). A major eddy system occurs in the Southern California Bight (SCB) south of Point Conception, and a second eddy system occurs in Sebastian Vizcaino Bay, Baja California. Wind-driven coastal upwelling occurs along the more exposed sections of coastline, particularly at headlands, cooling the inshore area and adding nutrients to the already rich

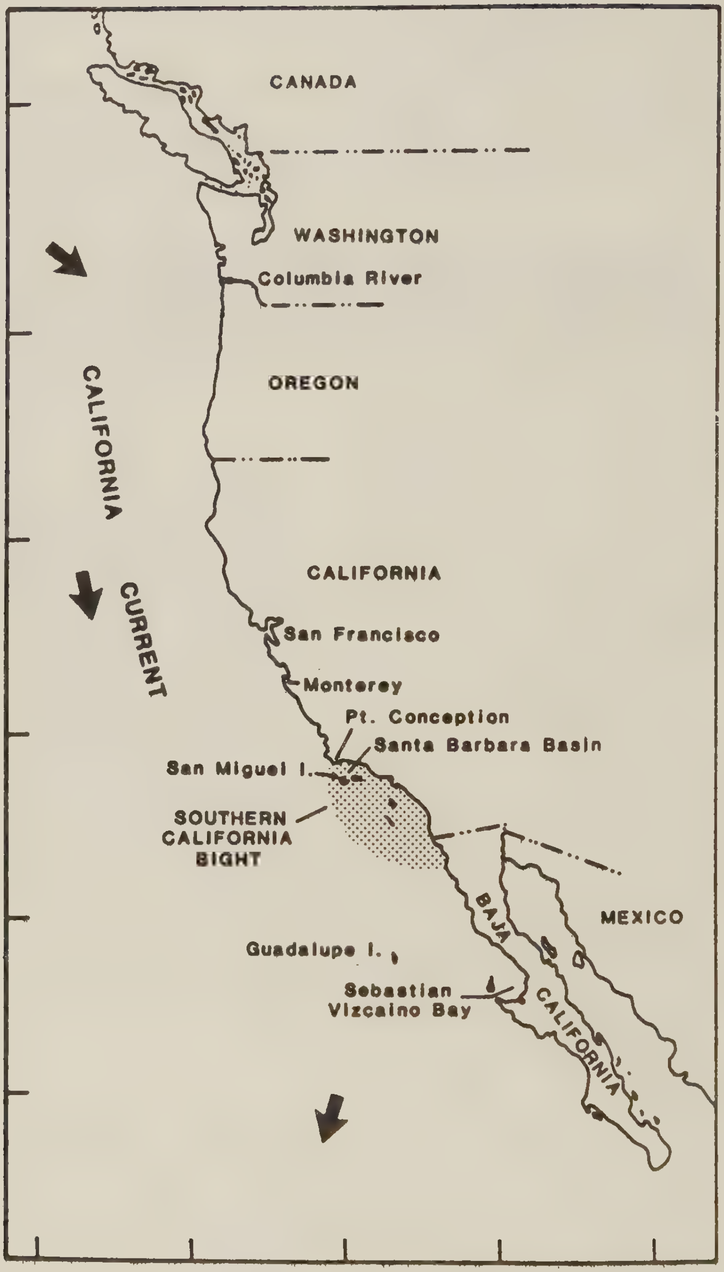
CANADA
WASHINGTON
Columbia River
OREGON
CALIFORNIA CURRENT
CALIFORNIA
San Francisco
Monterey
Pt. Conception
Santa Barbara Basin
San Miguel I.
SOUTHERN CALIFORNIA BIGHT
MEXICO
BAJA CALIFORNIA
Guadalupe I.
Sebastian Vizcaino Bay

Figure 4.1. Map of the California Current region, with some place names which are referred to in the text.

waters being advected southward from the northeast Pacific. The SCB is a special habitat within this system, being warmer and influenced by numerous islands and banks. Most of the remainder of the California Current has little interaction with the seabed due to a relatively narrow continental shelf. Some useful reviews of California Current oceanography are Reid et al. (1958), Hickey (1979), and Parrish et al. (1983).

The main body of the California Current lies offshore and contains an abundance of lower trophic level organisms; this area has been studied extensively by biological oceanographers who have benefited from regular surveys made by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) since 1950. From the viewpoint of this volume, more emphasis must be placed on the inshore regions, especially the SCB, where higher trophic level organisms such as fish, marine mammals, and seabirds abound. It is these organisms that usually are of most concern to management, as they play a visible role in human culture and economy.

PREINDUSTRIAL CONDITIONS

The natural state of the California Current ecosystem was almost certainly one of substantial variability at all time scales. Anaerobic sediments in the Santa Barbara Basin of the SCB contain a rich record of recent fossil remains, particularly fish scales from the past few centuries. The annual layering of these sediments allows precise dating, and enabled Soutar and Isaacs (1969, 1974) to compile time series of scale deposition rates which may be interpreted as rough indexes of abundance (Figure 4.2). While the process of scale deposition and relation to the source population is poorly defined, scale deposition rates tend to agree with well-documented changes in commercial fish abundance since 1930, providing some credibility for their interpretation (Soutar and Isaacs, 1974; Smith, 1978; Lasker and MacCall, 1983).

Another demonstration of long-term variability is given by Hubbs (1948), who interprets lists of fish species collected by the Pacific Railroad Survey in 1853-1857 and by Jordan and Gilbert in 1880. Many tropical species are shown which are exceedingly rare or unknown in modern experience; other species normally restricted to the SCB and southward are reported as being abundant in Monterey Bay, central California. Douglas (1980) has used tree-ring data to reconstruct past sea surface temperatures off California, and the period 1841-1859 appears anomalously warm. Northward faunal shifts are known to be associated with oceanic warming off Califonia (Hubbs, 1948; Radovich 1961), but

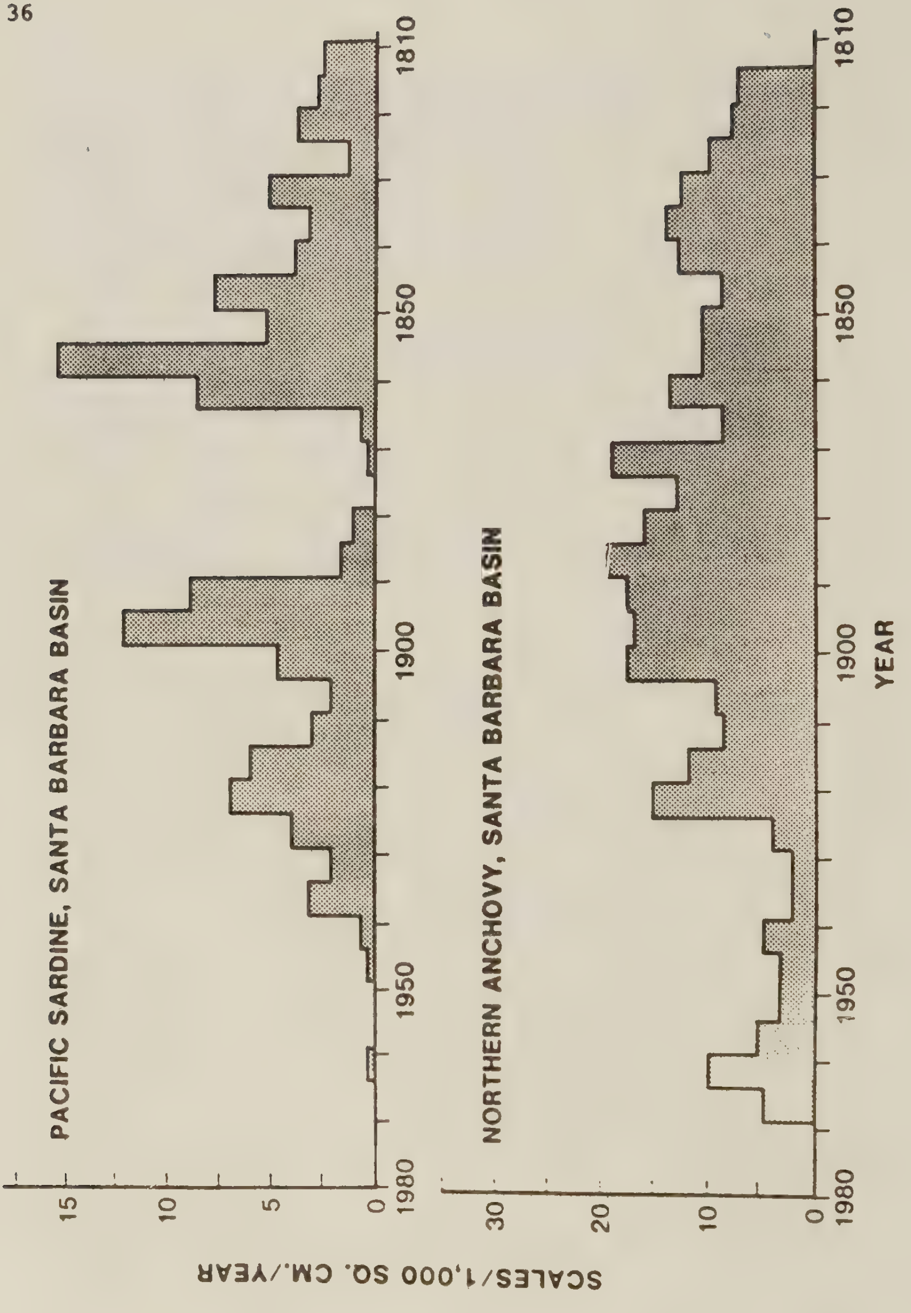

Figure 4.2. Recent scale deposition rates for Pacific sardine and northern anchovy (from Soutar and Isaacs, 1974).

nothing of the magnitude and duration experienced in the mid-1800s has been seen since then.

Marine mammal abundances were severely impacted by the influx of Europeans in the 1800s. The major fur bearers--northern fur seal (*Callorhinus ursinus*), Guadalupe fur seal (*Arctocephalus townsendii*), and California sea otter (*Enhydra lutris*)--were quickly reduced to near-extinction, as were the northern elephant seal (*Mirounga angustirostris*) and the California gray whale (*Eschrichtius robustus*) which were rendered for their oil. Other pinnipeds less sought for commercial purposes, such as the California sea lion (*Zalophus californianus*), suffered from prolonged hunting before concern turned to predator control for the marine fisheries.

Seabirds also were impacted by the influx of Europeans, particularly following the gold rush of 1849. Seabird eggs were harvested for food, and disturbance of the breeding colonies caused further reproductive difficulty. In 1854 common murres (*Uria aalge*) numbered about 400,000 on the Farallon Islands near San Francisco, judging by the magnitude of the annual egg harvest (Ainley and Lewis, 1974). As recently as 1959 these birds numbered only about 6,000, but their population has since recovered to 60,000 as a result of protection from disturbance (Sowls et al., 1980). Changes of seabird abundance in other locations are poorly documented, but most accessible colonies near human population centers were probably adversely impacted.

Except for the few fishes represented in Soutar and Isaacs' sedimentary record, it is particularly difficult to reconstruct the prehistoric state of the California Current ecosystem. Abundances of animal remains in prehistoric middens suggest that the Guadalupe fur seal may have been the dominant pinniped in southern California (Walker and Craig, 1979). Ironically this species does not presently reproduce in southern California although it has recovered somewhat on Guadalupe Island where it was "rediscovered" only 30 years ago (Antonelis and Fiscus, 1980). The northern fur seal has a southern rookery on San Miguel Island where waters are cool due to strong upwelling off Pt. Conception. Their prehistoric abundance at this location may have been high, and they probably were quite important in the northern part of the California Current, with large numbers of subadult females migrating southward from the Pribilof Islands. A major peak in Soutar and Isaacs' (1974) scale deposition rate for Pacific hake (*Merluccius productus*) coincides with peak harvests of fur seals at the Pribilof Islands in the late 1800s (Anon., 1977).

Aboriginal impacts on natural resources are usually thought of as being in approximate equilibrium. McEvoy (1979) concludes that aboriginal salmon harvests in northern California approached maximum sustainable yield (regulated by a variety of cultural mechanisms) and greatly exceeded harvests sustained by later industrial fisheries. Impacts on most other marine species were relatively small. An apparent exception is Chendytes lawi, a flightless marine duck with a well documented evolutionary lineage over the last 2 million years in California (Warter, 1978). The most recent remains from Indian middens have been dated at less than 3,780 years B.P. (Morejohn, 1976). As Morejohn observes:

> The high frequency of occurrence of bones of this species at one Indian midden clearly implicates early California aboriginal man as playing an important role in its extinction.

RESOURCE VARIABILITY IN THE 20th CENTURY

Commercial fisheries in California have been studied and monitored closely since the early part of this century, but they have been managed very little. Recreational fisheries, which have a major impact on many California fish stocks, have been monitored since the late 1940s, although substantial fishing pressure has existed for much longer. Mexican fisheries probably had a small impact on California Current fish stocks prior to the 1960s, and some segments of that industry have grown substantially in the last decade. Marine mammals and seabirds were not extensively monitored or studied until the 1970s when public awareness increased and several environmentally oriented acts were promulgated by the U.S. and California legislatures. This section discusses the variability of these California Current resources, and the subsequent section discusses their management.

The collapse of California's Pacific sardine (Sardinops sagax caerulea) fishery in the late 1940s set a well-documented pattern later followed by many of the world's coastal pelagic fisheries. However, the appearance of collapse may be an artifact of scale: A logarithmic plot of historical sardine abundances (Figure 4.3) indicates a prolonged exponential decline with a remarkably constant average rate of decay, about -0.2/yr. MacCall (1983) interprets this as a constant average rate of overexploitation, with harvests exceeding replacement levels by about 18% over the entire history of the fishery. Also, the variability about the trend in Figure 4.3 is of roughly constant magnitude indicating constant proportional variability

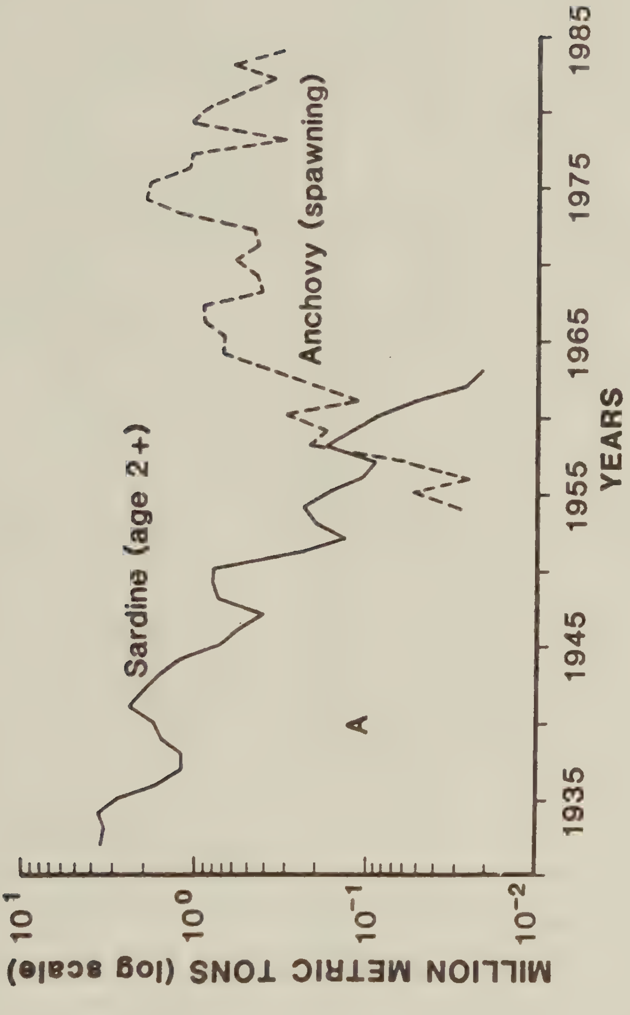

Figure 4.3. Time series of sardine (age 2+) and anchovy spawning biomass (log scale) off California and northern Baja California. "A" denotes approximate anchovy spawning biomass in 1940-1941 (interpreted from Smith, 1972). Sardine biomasses are from Murphy (1966) and MacCall (1979); anchovy biomass are from MacCall and Methot (1983).

from environmental fluctuations, and suggesting that difficulties experienced near the end of the fishery were not unusually severe. Removal of a major component such as the Pacific sardine (unexploited biomass averaging about 3 million tons) from the California Current food web would presumably have measurable effects on other components of the ecosystem. It is surprisingly difficult to identify those putative effects.

The northern anchovy (*Engraulis mordax*) is commonly thought to be a competitor with the sardine. The circumstantial evidence of similar food habits and a large increase in anchovy abundance following the decline of the sardine (Figure 4.3) has often been cited as proof of competitive replacement (e.g., Odum, 1971). However, the increase in anchovy abundance lagged the sardine decline by nearly a decade, and Smith's (1972) evidence of a relatively large anchovy biomass in 1940, when sardines were abundant, is often overlooked. A direct interaction between the two species has been demonstrated by Santander et al. (1983) in Peru, where anchovies and sardines are mutual predators on their eggs and larvae; a similar relationship should occur in California. Possible competition for food is suggested by Lasker and MacCall (1983), who showed that anchovy scales from Soutar and Isaacs' anaerobic sediments are significantly smaller (implying smaller anchovies) when sardine scale deposition rate is high. However, recent observations weaken the hypothesis of strong interaction between the two species: Mean size of anchovies has declined drastically since the mid-1970s due to causes that cannot be attributed entirely to the increased fishing pressure. At the same time, Pacific sardines are showing signs of increase, but are still very scarce. If sardines were more abundant, the increase in sardine abundance would be thought to be the cause of the decline in anchovy mean size, but because sardines are presently an insignificant component of the trophic system, these phenomena must be independent results of another, presumably environmental influence. As Daan (1980) concluded in a general review of replacement phenomena, the case is very unclear for anchovy having competitively replaced the sardine in California.

Due to a string of very strong year classes, abundance of Pacific mackerel (*Scomber japonicus*), elsewhere known as chub mackerel, in the 1930s may have greatly exceeded average virgin stock levels (Figure 4.4). Over the following years spawning success (recruits per spawner) varied with a distinct 6- to 7-yr cycle which ended with severe depletion of the resource about 1965. A moratorium on fishing during the 1970s was successful in rehabilitating the resource, which

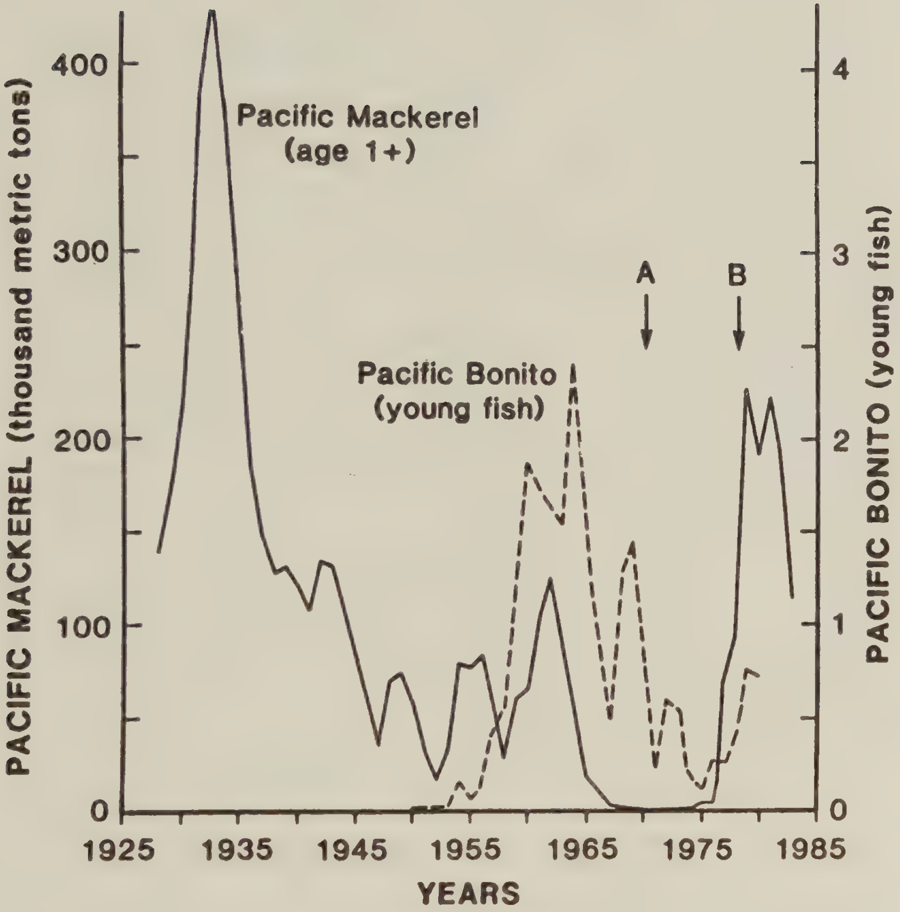

Figure 4.4. Time series of Pacific mackerel total biomass (age 1+) and Pacific bonito recreational catch per effort (fish per angler-trip). "A" denotes beginning of Pacific mackerel fishing moratorium, and "B" denotes re-opening of the fishery. Pacific mackerel biomasses to 1969 are from Parrish and MacCall (1978); bonito catch per effort is from Collins et al. (1980).

rebounded by producing the largest year class (1978) in the history of the fishery (Klingbeil, 1983). Surprisingly, the cyclic spawning success seen consistently in the 30 yr prior to collapse has not been evident in the erratic pattern of the recovered resource.

Pacific bonito (Sarda chiliensis) have long been seasonal visitors to California waters, with large northwardly migrating adults appearing in the SCB in the late summer and fall. However, an apparently self-sustaining population seems to have established residence in California only since the late 1950s, perhaps as a result of the oceanic warming of 1958-1959 (see Collins et al., 1980, for a complete review). Abundance has declined since the early 1960s (Figure 4.4). Some of that decline must be attributed to the commercial fishery which began harvesting bonito in 1966, but sustainability cannot be expected from a resource which has only recently come into existence. The bonito stock in the SCB seems to be a marginal population that hovers near the edge of viability. One hypothesis for its existence is that warm-water discharges from power generating stations have provided overwintering refuges for fish that would normally migrate southward (Collins and MacCall, 1977).

No substantial fishery has developed for jack mackerel (Trachurus symmetricus) in California or Mexico. A small fishery for young fish has existed since 1950 but the industry has had difficulty marketing the product. Much of the biomass consists of large adults inhabiting oceanic waters from the tip of Baja California to the Aleutian Islands, and as much as 1500 km offshore. These fish may exceed 30 yr of age, and stock size may be around two million tons (MacCall and Stauffer, 1983). Nearly all the spawning occurs in offshore oceanic waters, but subsequent young fish appear mainly in the SCB which serves as a nursery ground for a few years. Recruitment strength is highly variable (Figure 4.5), with seemingly periodic strong year classes tending to be isolated by several weak year classes. Age compositions for recent catches are unavailable, but the 1976 year class seems to be prominent, maintaining the pattern.

There are about 60 known species of rockfishes (Sebastes spp.) in the California Current, most of which are demersal and reside north of the U.S.-Mexican boundary (Miller and Lea, 1972). Some of the more pelagic rockfishes such as shortbelly (S. jordani), bocaccio (S. paucispinis), and chilipepper (S. goodei) potentially interact with shallow schooling pelagic fishes such as anchovy and sardine. Abundance of rockfish larvae has been monitored by the CalCOFI ichthyoplankton surveys since the early 1950s, and a few species such as shortbelly and bocaccio are

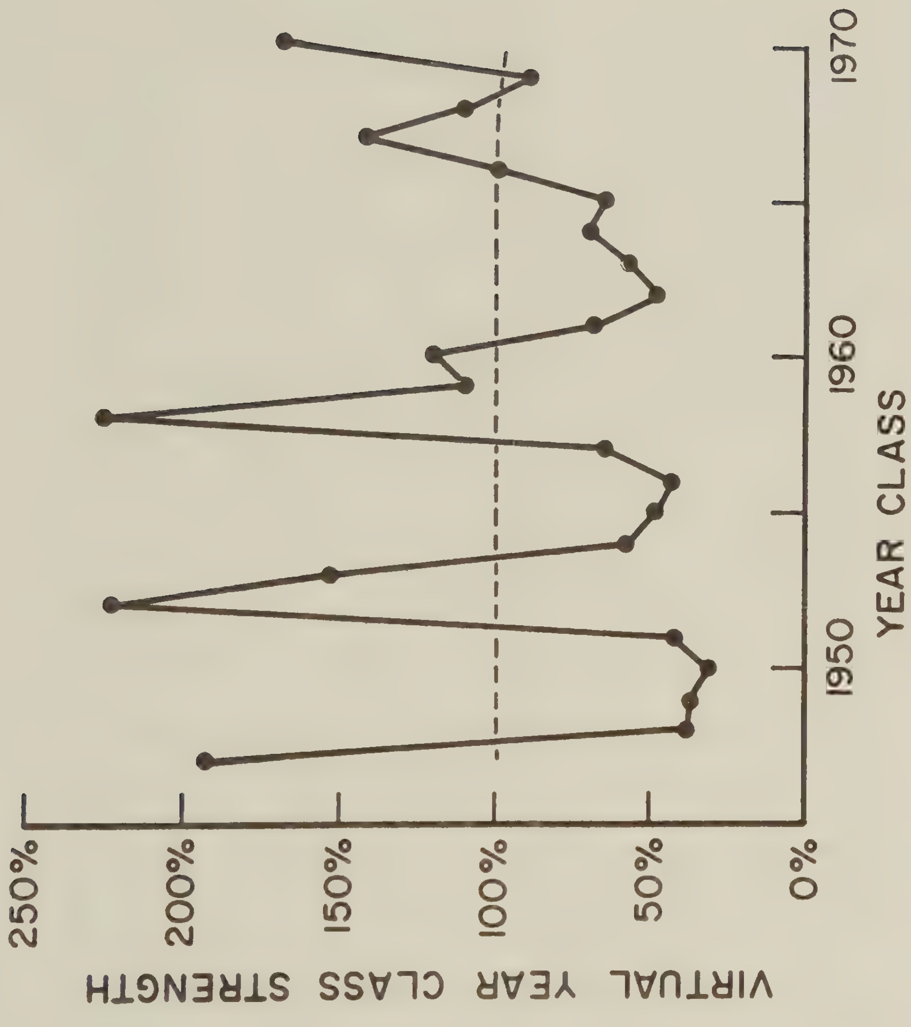

Figure 4.5. Relative recruitment strengths of jack mackerel year classes in southern California (From MacCall and Stauffer, 1983).

identifiable as small larvae. Abundance of adult shortbelly rockfish appears to be several hundred thousand tons, based on acoustic-trawl surveys (inferred from Lenarz, 1980), and, as this species contributes about one-tenth of all *Sebastes* larvae in the CalCOFI surveys, total rockfish abundance must amount to several million tons. Relatively few species of rockfish are sufficiently abundant, vulnerable, and desirable, to be the object of major commercial or recreational fisheries.

Abundance of rockfish larvae has varied substantially over the last 30 yr. In southern California, where sampling has been the most consistent, the data show three distinct periods (Figure 4.6). The early and recent periods appear fairly stable, with a suggestion of higher abundance recently. The anomalous middle period is initiated by the oceanic warming of 1958-1959 when larval abundances dropped severely. Unlike most other fish species, rockfish larval abundances did not recover immediately following the return to normal oceanic conditions in the early 1960s, but took about ten years to recover to previous levels. It is unclear to what extent the depressed larval abundances were due to decreased adult abundance or to decreased fecundity of those adults. There is no trend in shortbelly rockfish larvae (Figure 4.6) despite large changes in abundance of potentially competing anchovy and sardine. Abundance of bocaccio larvae (Figure 4.6) seems to parallel changes in abundance of anchovy, but the reason is not known; however, adult bocaccio are large fish, and are probably predators of anchovy.

Most of the larger predatory fishes are migratory. The temperate tunas, bluefin (*Thunnus thynnus*) and albacore (*T. alalunga*) visit the California Current as 1- to 3-yr-old fish in late summer during their transpacific migrations. Catch rates of both species have declined from peak levels of the 1960s (Hanan, 1983; Laurs, 1983). Many predatory fishes migrate along the coast, wintering in Baja California waters, and moving northward into California waters in the summer. Most of these species are now at low abundance relative to those of the early 1900s. Intense commercial and recreational fisheries on white seabass (*Atractoscion nobilis*) and California barracuda (*Sphyraena argentea*) have resulted in very low abundance of these species. A contraction of range is evident for white seabass, which formerly supported a commercial fishery in San Francisco, but now occurs only south of Pt. Conception (Methot, 1983; also see reviews by Collins, 1981; and Vojkovich and Reed, 1983, for white seabass; and Schultze, 1983, for barracuda). Yellowtail (*Seriola*

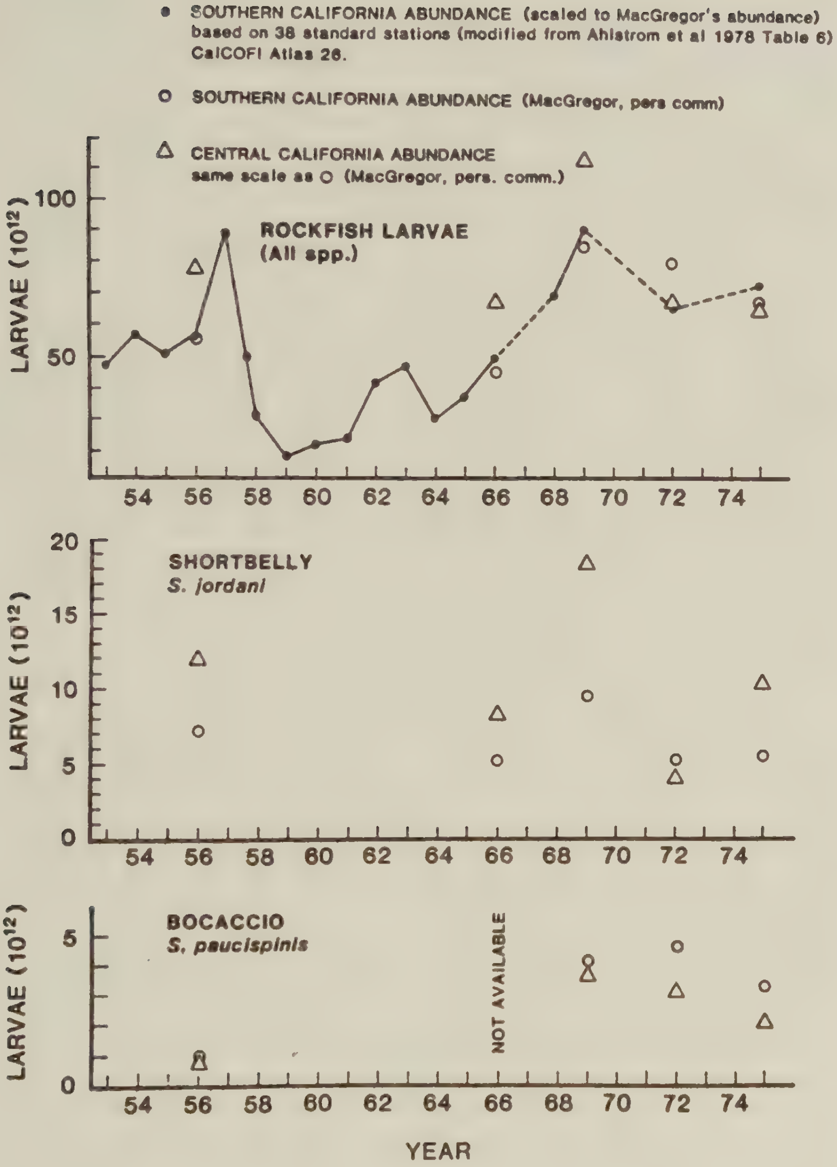

Figure 4.6. Abundances of larval rockfishes off California. Abundance indexes were provided by J. MacGregor, Southwest Fisheries Center, La Jolla, CA.

lalandei) is a popular target of southern California recreational fishermen who take mainly the northward migrants that reach the SCB. Yellowtail appeared to have increased in abundance since the end of the commercial fishery in the 1950s (MacCall et al., 1976), but have recently declined due to several years of poor recruitment (Crooke, 1983). Intense fisheries for thresher sharks (Alopias vulpinus) and bonito sharks (Isurus oxyrinchus) have developed recently (Cailliet and Bedford, 1983), and may be expected to reduce rapidly the abundance of those low fecundity species (cf. Holden, 1977). The pre-fishery abundance of predatory fishes is difficult to estimate, but should be severalfold larger than their peak historical harvests, perhaps by one or two hundred thousand tons. Their present-day abundance is probably 10 to 25 percent of the original level, and the corresponding reduction in prey consumed should have had a beneficial effect on net productivity of the latter species.

Many other species play important roles in the California Current ecosystem. For example, market squid (Loligo opalescens) supports a commercial fishery, and is a major component of many predators' diets. Unfortunately, little is known about the abundances and variability of these species.

MULTISPECIES CONSIDERATIONS

Our knowledge of multispecies interactions is surprisingly limited in view of our extensive knowledge of the California Current. As was suggested in the preceding discussion, it is difficult to assess the impact of the loss of the sardine from the ecosystem. Both natural variability and fisheries have affected other components of the ecosystem, and responses are often indirect and confounded. Our knowledge has been gained mostly since the beginning of the CalCOFI Program in 1950, a period in which the sardine has had little biological influence. While it seems reasonable to assume that loss of the sardine has had a significant impact on the ecosystem, the alternative hypothesis should also be considered: The ecosystem may be well adapted to a highly fluctuating sardine abundance, and its disappearance may have had relatively few identifiable effects.

In a few cases, predator requirements have been defined quantitatively. The brown pelican (Pelecanus occidentalis californicus) is a designated "endangered species" due to pesticide contamination and associated reproductive failure about 1970, a condition from which the California colonies have largely recovered (Anderson et al., 1975; Anderson and Gress, 1983). The relationship between pelican breeding success and anchovy abundance (its main prey) is well-established (Figure 4.7, also see Anderson et al., 1980, 1982). If sardines once again become abundant, brown pelicans are likely to include them in their diet and should enjoy higher breeding success and less dependence on the anchovy (cf. Crawford and Shelton, 1978). In this context it is relevant that brown pelicans ceased breeding effectively at Pt. Lobos, near Monterey, at the same time that the Pacific sardine fishery failed (MacCall, in press). The relationship between brown pelican breeding success and anchovy abundance is recognized explicitly in the Northern Anchovy Fishery Management Plan developed by the Pacific Fishery Management Council (MacCall et al., 1983). Direct relationships between seabird reproduction and anchovy abundance have been shown also for western gulls (Larus occidentalis) and Xantu's murrelets (Endomychuura hypoleuca) by Hunt and Butler (1980), and for elegant terns (Sterna elegans) by Schaffner (1982). Despite their relatively high metabolic requirement, seabirds probably are not abundant enough in the California Current to have a major long-term impact on abundance of prey fishes. However, at times, seabird impact on forage may be large. For example, Wiens and Scott (1975) estimate that the millions of sooty shearwaters (Puffinus griseus) passing along the Oregon coast during their late summer southward migration may consume over 450 tons of anchovies per day, and larger quantities may be assumed for the much longer California coastline.

Pinnipeds consume large quantities of fish, and are increasing at a rapid rate in California. The approximately 70,000 California sea lions have been estimated to consume 100,000 to 300,000 tons of fish, and the 40,000 elephant seals may annually consume 400,000 to 1,000,000 tons, mostly of demersal fish (DeMaster, 1983). Daily rations are well known for pinnipeds, due to experience with captive animals, but the response to fluctuations in abundance and species composition of forage in the ocean is poorly known. Per capita reproductive rates of pinnipeds appear relatively constant except for severe declines during oceanic warmings such as 1982-1983.

A particularly difficult issue is the relationship between anchovy abundance and catch rates of large predatory fish. California's recreational fishermen strongly feel that abundant forage is necessary to attract large fishes to the region. Anchovies are certainly important to recreational fishing operations, being used as live bait, and anchovy schools provide visual clues to the location of predator fishes. The importance or value of these uses of anchovy is very difficult to quantify, but recognition of the large

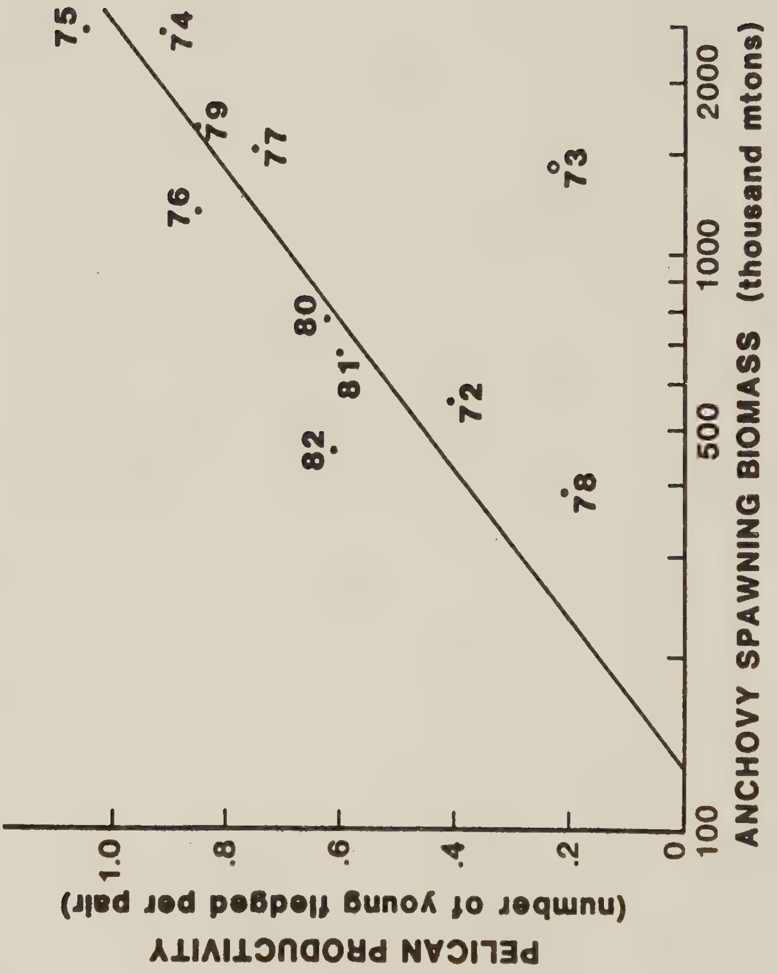

Figure 4.7. Relation between brown pelican productivity (Anderson et al., 1980, 1982) and anchovy spawning biomass (from MacCall et al., 1983). The 1981 and 1982 productivity values are unpublished data.

recreational fishing constituency in California has influenced anchovy harvesting policy, and constrained U.S. commercial fishery development in the early 1970s. More recently, the Pacific Fishery Management Council has chosen to pursue a harvest policy which seeks a moderate, relatively constant allowable anchovy harvest, and establishes a minimum level of anchovy abundance below which non-bait uses are curtailed (MacCall et al., 1983).

Multispecies considerations are operationally important to management of many species in California, although the biological basis of management remains single-species models. Incidental catches of non-target species are regulated, especially in the case of depleted stocks such as sardine and Pacific Ocean perch (Sebastes alutus). In order to prolong fishing opportunities, some fishing seasons have been established interactively. For example, in California, the anchovy reduction (fish meal) fishery ends on June 30, when summer live bait demand is high. The Pacific mackerel fishery opens on July 1, preserving continuity of opportunity for the California purse seine fleet (Klingbeil, 1983).

OUTLOOK

Developments in the California Current ecosystem and its management during the remaining years of the 20th century should be very interesting. The Pacific sardine recently has shown signs of increase (Bedford et al., 1983), although the resource presently remains severely depleted in the California Current. Recovery of depleted coastal pelagic resources often occurs suddenly, with production of a large year class. Examples are the strong 1976 and 1978 year classes of Pacific mackerel in California (Klingbeil, 1983) and the recent increase in sardines off Japan (Kondo, 1980). If recovery of the sardine is rapid, ecosystem effects may be somewhat easier to assess than they would be for gradual changes.

The major U.S. anchovy fishery produces fish meal, a high protein animal feed supplement which has declined in demand due to replacement by enriched soybean meal (Thomson, 1984). The Mexican fishery has grown since the mid-1970s, and Mexican domestic demand for fish meal is expected to remain strong. Consequently, the major harvest of anchovy now occurs south of the U.S.-Mexican border, where harvests are unregulated.

Pinniped populations are increasing rapidly, with some species increasing at over 10 percent per year, and interactions with fishermen are increasing disproportionately. Marine mammals are presently protected by the U.S. government under the Marine Mammal

Protection Act, but return of management to the individual states is being promoted. The debate between the preservationists and the fishermen is highly emotional, and the future course of marine mammal management in the California Current should be interesting to watch.

The greatest difficulty facing ecosystem management is the multitude of jurisdictions, often overlapping and conflicting, and each with its own objectives, responsibilities, and responsiveness. The portion of the California Current south of the U.S.-Mexican border is under Mexican jurisdiction, where some fauna such as marine mammals are protected, but fishery regulation is minimal. Access to Mexican waters by U.S. commercial fishermen has been severely restricted since 1982, which should have reduced fishing pressure on many species off Baja California. In California some species are managed by the federal government through the Pacific Fishery Management Council, while others are managed by state institutions, including the California legislature (most commercial fisheries) and the California Fish and Game Commission (recreational fisheries and some commercial fisheries). Marine mammals are managed by the U.S. Department of Commerce (and may be returned to state control), but seabirds are under the authority of the U.S. Department of the Interior. Despite this seeming confusion, coordination has been moderately successful when pursued on a single-species basis. Actual ecosystem management, if it were technically feasible, would be difficult to achieve unless management authority were better consolidated, with provisions for local representation and responsiveness. Such a consolidation appears unlikely in the foreseeable future.

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8661

CHAPTER 11

Rethinking Research For Fishery and Ecosystem Management

ALEC D. MacCALL
Fisheries Biologist
Southwest Fisheries Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
La Jolla, California

WHY DO RESEARCH?

It is appropriate to preface this discussion with some general comments on the objectives of, or justifications for, fishery or ecosystem research. Probably the most generally accepted justification for research is the prospect of improved management, whether it be for increased yield or value, or perhaps for a predictive capability which decreases risk. The assumption is the more we know, the more closely we can approach our management objectives. Unfortunately, this argument is at times perverted in order to postpone difficult decisions, or to rationalize poor management performance: "We don't know enough about the resource to..."

As we move from consumable resources to those which traditionally are not consumed (for simplicity, I call these "non-consumable"), such as seabirds and marine mammals, research is often justified by legislative mandate. Several U.S. legislative acts, such as the National Environmental Protection Act (NEPA), the Marine Mammal Protection Act (MMPA) and the Endangered Species Act (ESA) require an ecosystem understanding of interactions among species and impacts of man's activities. This category also includes progressive international treaties such as the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), which specifically calls for an integrated ecosystem approach to management. To some extent, these mandates include an accounting for indirect effects on consumable resources. For example, contaminants and habitat destruction addressed by NEPA affect both consumable and non-consumable resources. On the other hand, the MMPA includes fishery impacts on the food supplies and mortality of marine mammals, but in its intent of protection rather than management, excludes consideration of those mammals' impacts on fishery values. Importantly, these legislative mandates for management and protection of non-consumable resources have mostly focused on large, visible high-level predators (at least in the marine realm), and that is where most of the attendant research has been directed.

HOW MUCH RESEARCH?

Given the various justifications or motivations for conducting research, the equally important but difficult question remains as to how much research is appropriate. In the case of consumable resources, the value of research is potentially quantifiable. In keeping with the assumption that more information should allow closer approach to optimum utilization, we can draw two important quantitative inferences: First, there is a limit to the value of information, as the resource itself has a limit to the benefits it can provide under ideal management. Second, the value of information conforms to the rule of diminishing returns. Initial information on a resource is valuable in establishing reasonable expectations by management, whereas additional information serves mainly to refine the approach to optimum utilization. It is arguable whether there is a limit to information in the way that there is a limit to fishery value, but in any case, accumulation of useful information also conforms to the rule of diminishing returns as a function of cost.

The relationship between information, its cost, and fishery value is instructive (Figure 1). Given ideal management, maximum net value from a fishery (benefit less cost) is achieved at relatively low levels of information (Figure 1a). Here, ideal management is characterized as low-expectation, low-cost, and robust or self-limiting (low-risk). For example, the fleet size would be limited to that which is able to harvest an amount well short of the estimated maximum sustainable yield, and quota determinations, monitoring and enforcement would be avoided. Ideal management is somewhat of a fiction, but serves mainly to contrast with actual management (Figure 1b). Performance of actual management has been variable, but most often fishery value has been dissipated by excess fleet capacity (so-called "overcapitalization") and excess fishing pressure, placing the fishery on the descending limb of the production curve (i.e. increased fishing intensity leads to decreased average yield). Ironically, actual fishery management often has led to relatively low fishery value partially as a consequence of aggressively but haphazardly trying to maximize that value.

Information costs can be evaluated in terms of fishery economics: research is in effect a form of capital investment, and monitoring incurs an operating cost. From this viewpoint, actual management often tends to overinvest (or "overcapitalize") in information, and this habit has been a further source of dissipation of total fishery value. It is easy to see the forces which cause this problem: managers, researchers, and the various interest groups which vie for allocations of the resource all agree on the need for more information to support their individual arguments or interests. Researchers may claim that their work relates to management even when the connection is negligible—such claims may improve prospects for funding. The cost of the research is seldom a consideration; usually it is not borne by the interest group requesting it or benefiting from it, but rather by government agencies. Private interest groups may add to this total expenditure by hiring consultants to provide them with new information. Furthermore, such expenditures are often matched by the cost of government or opposing interest groups' responses to such efforts.

WHAT SHOULD WE DO?

Unfortunately, the solution is not simply to spend less on monitoring and research. Most present fishery management institutions have locked themselves into policies requiring intensive research and monitoring efforts. For example, most interpretations of the Magnuson Fishery Management and Conservation Act of 1976

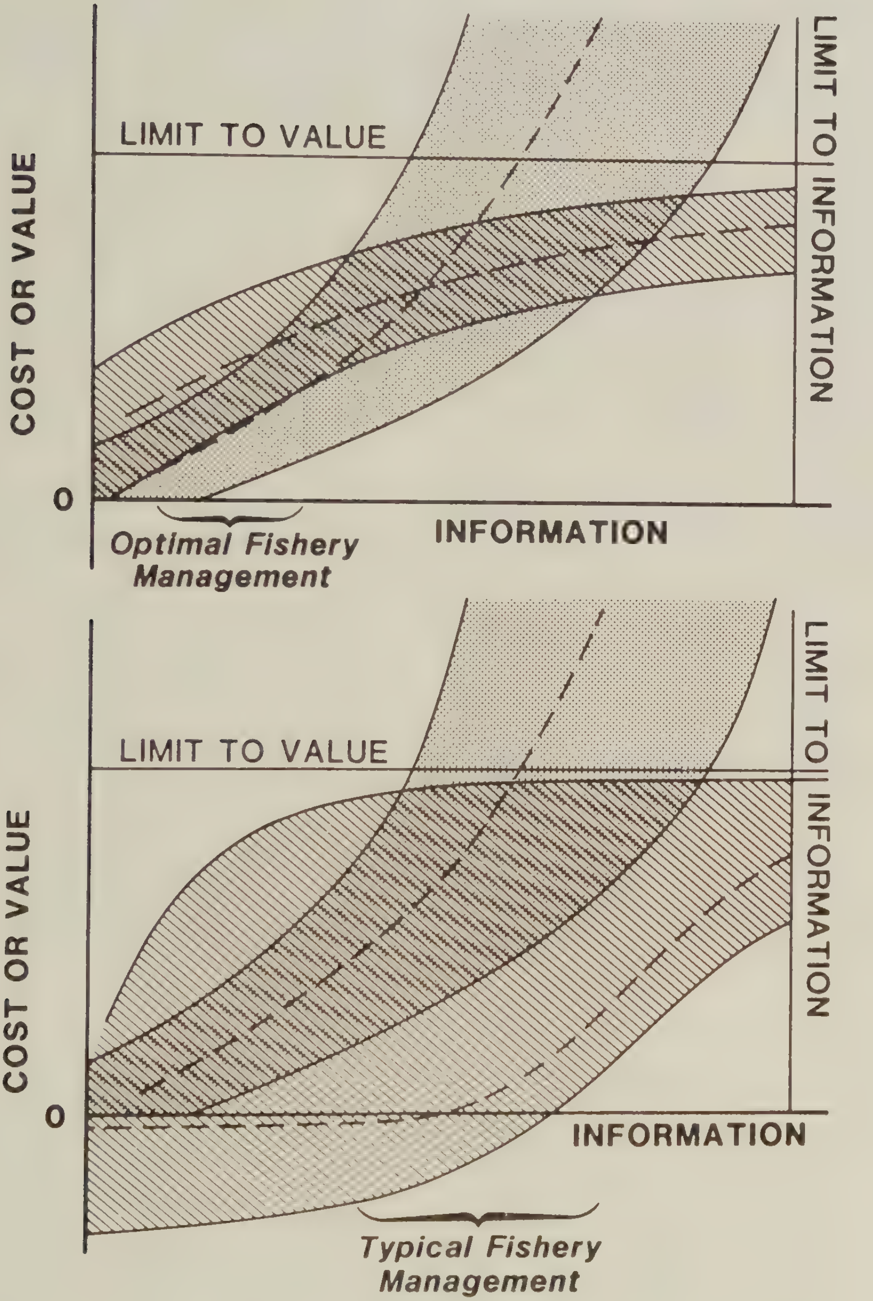
LIMIT TO VALUE
COST OR VALUE
LIMIT TO INFORMATION
0
INFORMATION
Optimal Fishery Management
LIMIT TO VALUE
COST OR VALUE
LIMIT TO INFORMATION
0
INFORMATION
Typical Fishery Management

Figure 1. The relationships among information, its cost (stippled region) and its benefit (hatched region) to fishery management a.(upper): "Ideal" management; b.(lower): "Actual" management. Shading represents the range of likely outcomes. Dashed line represents the most likely outcome.

(MFCMA) have required annual setting of harvest limits, quotas or allocations, with associated requirements of information on the status of the resource, harvests and concerns of relevant interest groups. Given the existing management framework, reducing the investment in information would incur substantial risk of further declines in fishery value due to subsequent misinformed or uninformed management decisions.

Within the context of this information model, there are two courses of action which promise to improve the cost-effectiveness of information and management. The first, and less likely of the two, is to change management toward a "low-information" system. The potential value realizable from low-information management is critically dependent on establishing the appropriate management expectations and institutions. I will not go into describing such institutions, except to say that they would be substantially different from those presently governing most U.S. fisheries, and most likely would be perceived to be non-democratic, or at least non-egalitarian, requiring substantial limitation on freedom to participate in the fishery. Some candidates for these management approaches are discussed elsewhere in this symposium.

The second course of action is to keep routine fishery monitoring and research to the minimum level necessary to meet immediate management needs, and to emphasize research aimed at better understanding the workings of the physical, ecological, and human systems surrounding these fisheries. I am defining routine research to be that which follows the existing cost vs. information curve in Figure 1. The alternative, or system-oriented research, is characterized by the potential to *shift*, rather than follow, either of the entire curves: to increase the information obtained at given cost, or to increase the fishery value realizable at a given level of information, opening up new management possibilities within the existing management philosophy. I emphasize the word "potential" in the above definition, as the latter kind of research naturally contains uncertainty as to its eventual utility. If its utility were proven in advance, most likely the research would already have been done.

The distinction between the two kinds of research is not clear. Also, the appropriate level of routine research and monitoring is difficult to determine. Beyond its use in current fishery management, routine information forms an important base for system understanding, further blurring the distinction between the two types of research. Perhaps it is easier to attempt to clarify the distinction by means of examples.

EXAMPLES OF SYSTEM-ORIENTED RESEARCH

Elsewhere in this symposium, I was informed that the Atlantic surf clam fishery is presently opened for a few hours, once a week, when a disproportionately large number of vessels descend on the resource. Accuracy of the details are unimportant to my example: currently the abundance is estimated annually, whereas it was also suggested in the symposium that this routine monitoring could reasonably be reduced to a bi- or tri-annual effort. This would be an improvement in the cost-effectiveness of routine research. However, if we consider a system view of the geography of surf clam productivity, we can hypothesize the following model which stands in contrast to routine homogeneous fishery models. Mobility of the resource occurs only during the planktonic phase, when the spawn diffuses along the coast. Clams are immobile once they settle. The edge of the population is determined by physical or competitive conditions, and clams at the edge of the population contribute very little to the population's productivity—their offspring are mostly lost to uninhabitable locations. Clams at the center of the population have the greatest probability of contributing surviving offspring because they are surrounded by inhabitable locations. This suggests that an unrestricted fishery could be allowed at the edges of the resource, and that the center of the population should be managed for maximum spawn production rather than maximum yield. Because of filter-feeding cannibalism, the density in the center might have to be reduced somewhat to achieve optimality. The point is that research dedicated to developing a geographic understanding of the system could lead to a rather different pattern of fishing within the present management philosophy, with an increase in realized productivity.

Some examples of system-oriented research on ecosystems include study of the cause and biological effects of prolonged changes in physical conditions. Bakun (In press) has shown some striking changes in the physical conditions off Peru (Figure 2). Changes of this kind, though perhaps not always this extreme, occur in all ecosystems. There is little reason to doubt that these physical changes are associated with changes in spawning and survival of fish eggs, larvae and juveniles, and hence sustainable yields. A system understanding will be necessary to replace the inappropriate static equilibrium yield models presently governing fishery management with models which account for these changes. A related type of ecosystem change is the apparent replacement of one species by another, for example, the anchovy-sardine "flips" which have occurred in California and Peru, and the replacement of herring by sand lance in the north Atlantic. To the extent that these replacements are mediated by interspecific competition, there are good prospects for improved, coordinated management; alternatively, if these replacements prove to be the result of largely independent responses to the physical changes described above, management will have fewer viable options.

The increasing concern over the effects of contaminants and habitat loss on fish production is not being answered by current simplistic single-species fishery models. Again, a system-oriented understanding is necessary to address these problems. An adequate model must contain a representation of the temporal and spatial structure of the population or ecosystem in order to estimate the impacts of local perturbations. These models may provide additional information useful to fishery or ecosystem management, as in the case of the surf clam model proposed above.

Another important reason for system-oriented research stems from the way we address management problems. Traditional academic research has a well-known method: after a problem is posed, the researcher conducts research, gaining *new* information by which the question is answered. It is very rare that management questions or problems can be solved by this method. After the management problem is posed, the fishery or ecosystem researcher must sort primarily through information which has *already* been gathered, such as time series of abundances. There is very little in the way of research to collect new information which can help in solving the problem. Thus our ability to answer management questions is constrained by existing knowledge, by the nature and quantity of past research. The information which will be of greatest long-range use in answering management questions will be gained by system-oriented research rather than by routine research devoted to "fine-tuning" current management.

The remainder of this discussion will focus principally on the research (and monitoring) needed to improve our understanding of marine ecosystems, rather than on research specifically intended to support fishery management. Nonetheless, fisheries are clearly elements of these ecosystems, and fishery research remains important to the discussion in several respects. Fisheries have demonstrated the capability to influence the target species' abundance, sometimes to the point of virtual elimination as a functional element of an ecosystem [this has been the case with the Pacific sardine (*Sardinops sagax*) off California]. Also, fisheries are one of the few ecosystem processes which are nominally under man's control. Indeed, fisheries represent ecological "experiments" of extraordinarily large scale, albeit without proper

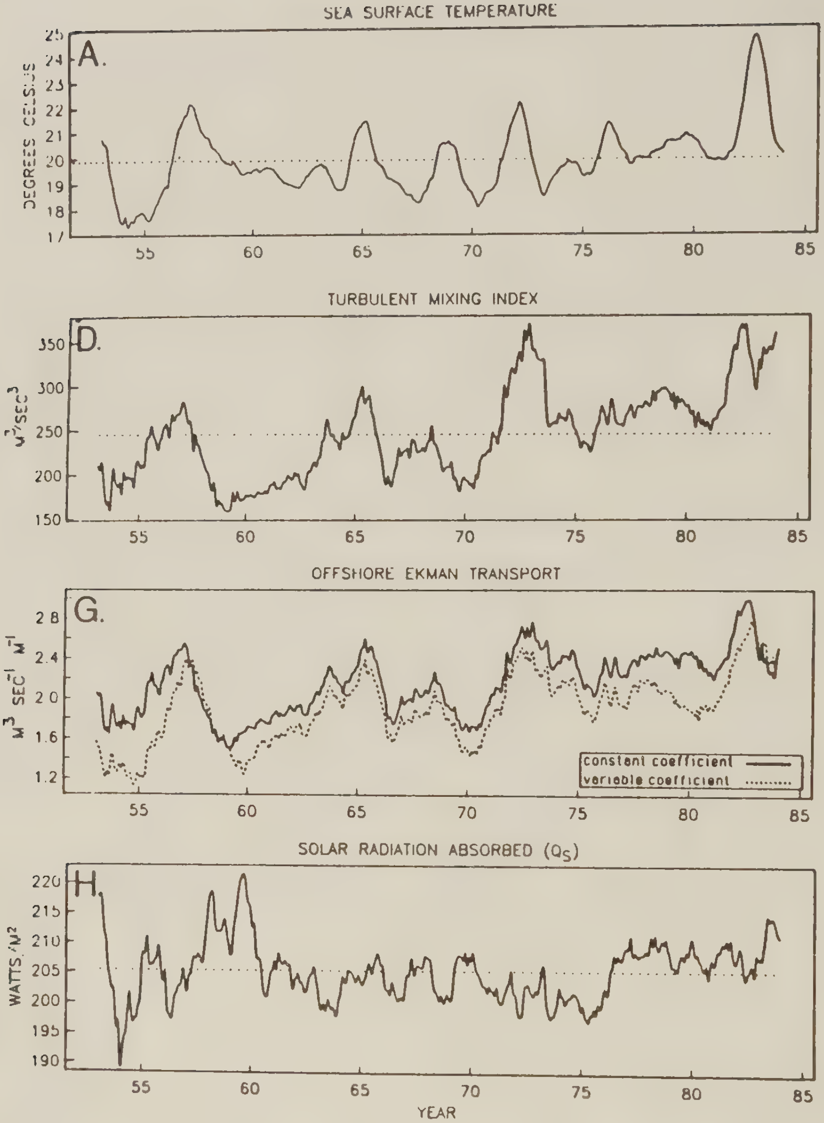

Figure 2. Time series of several physical oceanographic variables off the coast of Peru, showing changes in patterns over time (from Bakun, in press).

experimental controls. Finally, given that a fishery exists, it can be a source of large amounts of information at relatively low cost.

RESEARCH FOR MANAGEMENT OF MARINE ECOSYSTEMS

Ecosystem understanding necessarily requires a foundation of knowledge about the physical setting: physical oceanography, climatology etc. This foundation includes continuity of monitoring. Experience has shown that there are major shifts in physical patterns and associated biological patterns as progressively longer time periods are considered. Moreover, these shifts can be sudden, cannot be anticipated, and are difficult to recognize until well after the fact. Bakun (in press) presents time series of a suite of physical measurements for the Peruvian coast, some of which are reproduced in Figure 2. While the presence of dominant events such as the 1954-55 cold period and the 1982-83 El Nino have highly visible effects at the time they occur, the prolonged changes such as the shift in patterns following 1977 are more likely to cause changes in the structure of the ecosystem. Accordingly, it is important to supplement monitoring and research of the present system with information on the past behavior of the system. These sources include historical archives such as newspapers and journals, and natural chronological records such as tree rings and laminated sediments (Figure 3). It is often the biological information in these records that elucidates the changes that must have occurred in the physical system.

Another aspect necessary to understanding ecosystem functions is an appreciation of the historical development of man's impacts on the ecosystem. It is tempting to

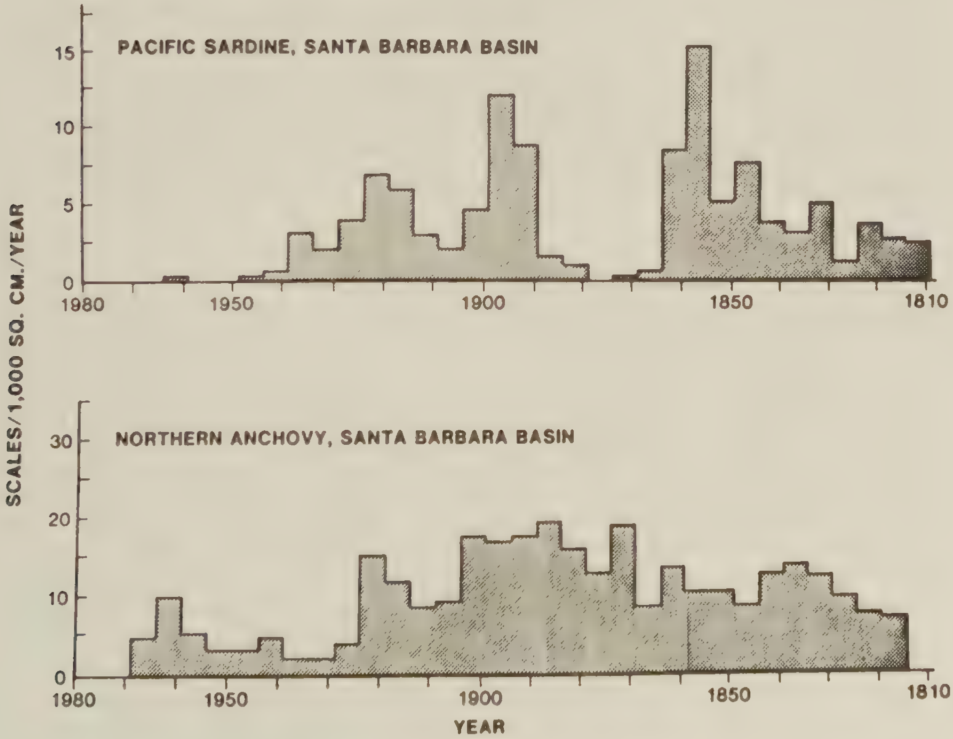

Figure 3. Recent scale deposition rates for Pacific sardine and northern anchovy off southern California (from Soutar and Isaacs 1974).

think of ecosystem impacts beginning with the major industrialization of fisheries in the early 20th century, but substantial impacts may have resulted from low-technology exploitation in the 18th and 19th centuries. For example, nearly all species of pinnipeds on the Pacific coast of the United States were reduced to very low abundances by the fur and oil trades during the last century and by predator control during the early decades of this century (MacCall 1986). Also, many of the large predatory fishes such as the tunas were depleted off California by 1920, when the tuna fleet began moving southward toward tropical waters. Natural mortality rates of the prey fishes must have been below the historical average as industrialized fisheries on these small pelagic fishes were expanding, a supposition which has never been addressed in the single-species fishery analyses and management.

A third area necessary as background to ecosystem research is biogeography. While it lacks glamour and is time-consuming and costly, an inventory of species, abundances and distributions (especially over time) is particularly valuable to multispecies or ecosystem management decision making. Of course the effort put into this work will vary according to species or trophic groups, both due to accessibility and interest on the part of researchers or managers. Government seems to be a necessary agent in this task, either by doing the work itself (e.g., the egg and larva surveys conducted in association with the California Cooperative Oceanic Fisheries Investigations, CalCOFI, Kramer et al., 1972), or by requiring such information to be part of environmental impact statements (EIS) or similar reviews. It is notable that fishery management plans developed under the MFCMA now must contain an EIS to meet the requirements of the NEPA.

Some marine ecosystems are unique, but most have several parallels. For example the eastern boundary currents off California, Peru, South Africa and North Africa contain remarkably similar assemblages of pelagic fishes, suggesting functional similarities in key oceanographic processes (Parrish et al., 1983). Comparative oceanography and biology of equivalent ecosystems not only provides insight into the workings of those ecosystems, but comparative history of exploitation may provide a rough replication of the massive fishery "experiments" mentioned above.

ECOSYSTEM MODELS

The value of constructing formal ecosystem models is debatable. As a tool to improve understanding of an ecosystem, the exercise often has been of greatest benefit to the builder himself. Unfortunately, this improved understanding has not easily been transferred to non-participants. As a tool to aid managerial decision-making, complicated ecosystem models tend to produce output which is too complicated to assimilate, especially if effects of random variability are included. Also, these complicated models tend to be sensitive to assumptions, such as the functional forms used to represent non-linear relationships. An example of this kind of uncertainty is the assumed form of the stock-recruitment relationship. Two popular stock recruitment models are the Ricker curve and the Beverton-Holt curve. These two curves are shown in Figure 4, which is taken from two well-known publications. Our uncertainty is demonstrated by the fact that two well-respected fishery experts have independently based these curves on the same data! While the two curves are about equally reasonable fits to these data on North Sea plaice, the corresponding anticipated patterns of population growth and stability are quite different. For management purposes, accurate and easily interpreted analyses usually are best produced by a much less complex model which is designed specifically to address the particular issue. Of course there are some issues, such as ecosystem stability and reversibility of species declines, which may require very large and complicated models; accordingly, definitive answers should not be expected. Beddington (1986) provides a useful discussion of this problem.

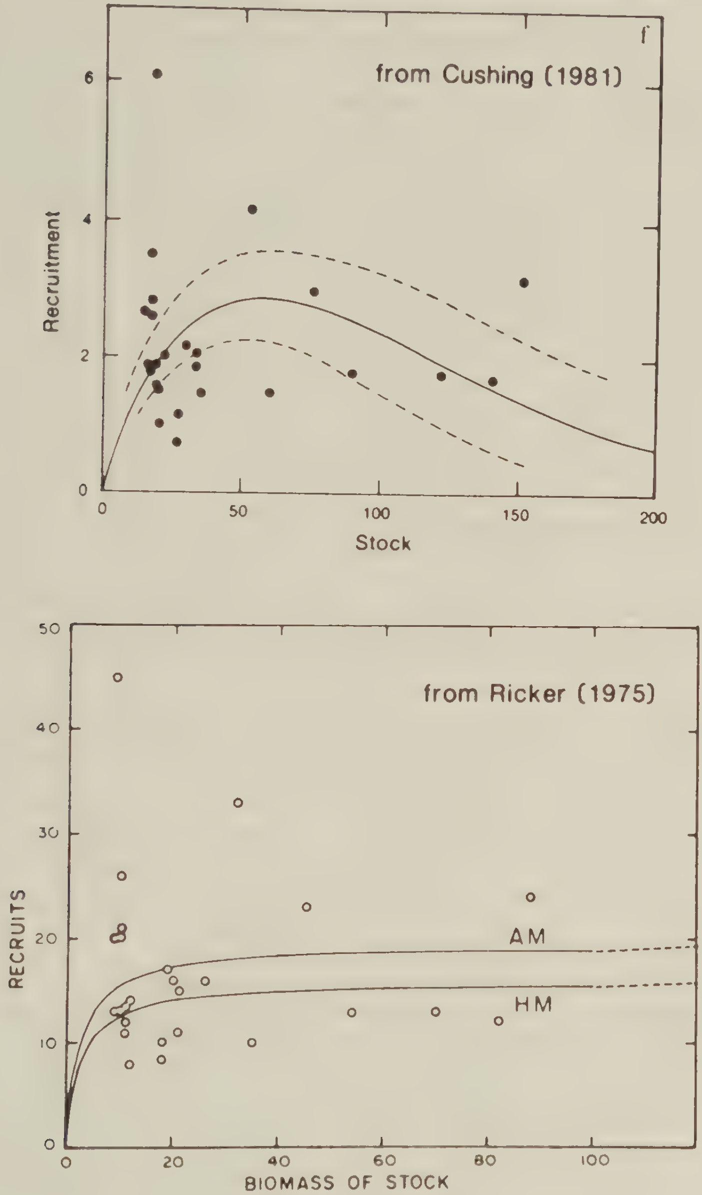

Figure 4. Demonstration of uncertainty in functional relationships: Independent fitting of two different stock-recruitment relationships using the same data on North Sea plaice.

The two most successful (or at least the most ambitious) marine ecosystem models have been Laevastu's Bering Sea model (Laevastu and Larkins 1981), and Ursin's North Sea model (Andersen and Ursin 1977). The two models represent rather different approaches to the problem, and require somewhat different kinds of background research and input data. The Bering Sea model is a compartmentalized accounting model, whereas the North Sea model is constructed of simultaneous differential equations. Thus the Bering Sea model emphasizes information on states while the North Sea model emphasizes information on rates, although the two models overlap substantially in their requirements. These large models have tended to be opaque to outside observers, and the extensive "tuning" of parameters which is required to obtain reasonable model behavior can hide serious deficiencies in our knowledge. Both of these models have had the advantage of portraying relatively closed, landlocked ecosystems, unlike the open systems found along continental coastlines or in mid-ocean. A satisfactory structure for ecosystem models of open marine systems has yet to be developed.

A much less ambitious model consists of a static input-output budget for various trophic components of an ecosystem. This would seem to be a minimum requirement for ecosystem understanding, forming the basis for estimating fluxes and perhaps carrying capacities for individual trophic levels or groups. Given the biomass in each trophic category, inputs can be calculated from information on energetics or food consumption, while outputs can be calculated from mortality rates. The matrix can be constructed on the basis either of inputs or of outputs, but can be considered satisfactory only if the two approaches agree, which seldom has been the case even for individual trophic categories. Bergh (1986) developed a trophic budget for the Benguela Current system off South Africa (Figure 5), based on a Delphi method survey of experts' opinions. A severe difficulty, which is common to the study of all marine ecosystems, was his inability to obtain reliable estimates of abundance and rate parameters for the squids, which by any account must be a major element in the system.

A common problem in these models is an apparently insufficient supply of prey. Green (1978) attempted such a budget for the California Current, as a starting point for modeling the effects of fisheries on the carrying capacity of marine mammals, but found that estimated fish and squid production could not meet estimated predator needs. Given that many of those predators, especially pinnipeds, have steadily increased in abundance, she concluded that the imbalance was erroneous, and that current knowledge could not support the modeling effort. Hunter and Lynn (Southwest Fisheries Center, in prep.) have estimated total anchovy (*Engraulis mordax*) predation by mackerel (*Scomber japonicus*) in southern California, and again, estimated anchovy consumption by this predator alone nearly exceeds the total abundance of anchovies. It is clear that substantial uncertainty exists in all three quantities appearing in each cell of the matrix--abundance, consumption (input rate) and mortality (output rate)--but the consistent direction of the imbalances is disturbing. Hunter and Lynn suspect that the mackerel obtained from fishery catches are more likely to have been feeding on anchovies than the average mackerel in the population, thus biasing the samples. In the past, similar discrepancies were perceived for lower trophic levels (e.g., zooplankton vs. phytoplankton, phytoplankton vs. carbon fixation), but these are now being resolved (R. Eppley, Scripps Institution of Oceanography, pers. comm.). The keys to improved understanding have been better knowledge of rate processes, and better accounting for spatial and temporal patterns of variability. Spatial distributions of most marine organisms are characterized by a high degree of contagion (patchiness); trophic interactions must be similarly patchy, and trophic rates may be influenced as much by the spatial variance as by the mean of a species' density.

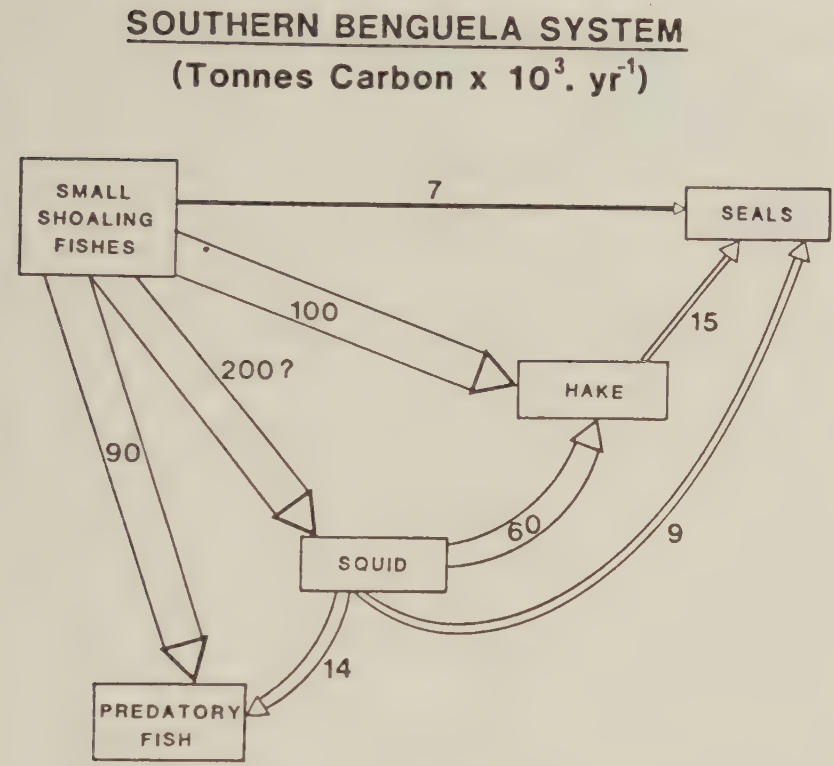

Figure 5. A trophic budget for the Benguela Current (from Bergh 1986).

OPERATIONAL CONSIDERATIONS

The expense of ecosystem research requires that surveys and sampling be planned for efficiency, but with emphasis on multiple purpose activity. These two objectives can conflict, as can be seen in the contrast between pelagic fishery landings, which tend to include few species but are conveniently centralized, and landings by demersal fisheries, which often include many species but are geographically diffuse (Figure 6). Another barrier to multiple purpose activity is institutional jurisdictions. For example, the National Marine Fisheries Service has responsibility for marine fishes and marine mammals, but not for seabirds, which are the responsibility of the U.S. Fish and Wildlife Service. Even within agencies, there may be psychological barriers between traditional fishery researchers who subconsciously promote consumptive uses of fish, and marine mammal or seabird biologists who stress the role of fish as forage.

An interesting possibility for low-cost ecosystem monitoring is the use of "indicator species." The reproduction or physiological state of some predators may be closely tied to the availability of prey. For example, the reproductive success of brown pelicans (*Pelecanus occidentalis californicus*) in southern California closely tracks the abundance of northern anchovy, its primary forage (Anderson et al. 1982, Figure 7). Similarly, changes in guano production by seabirds in South Africa and

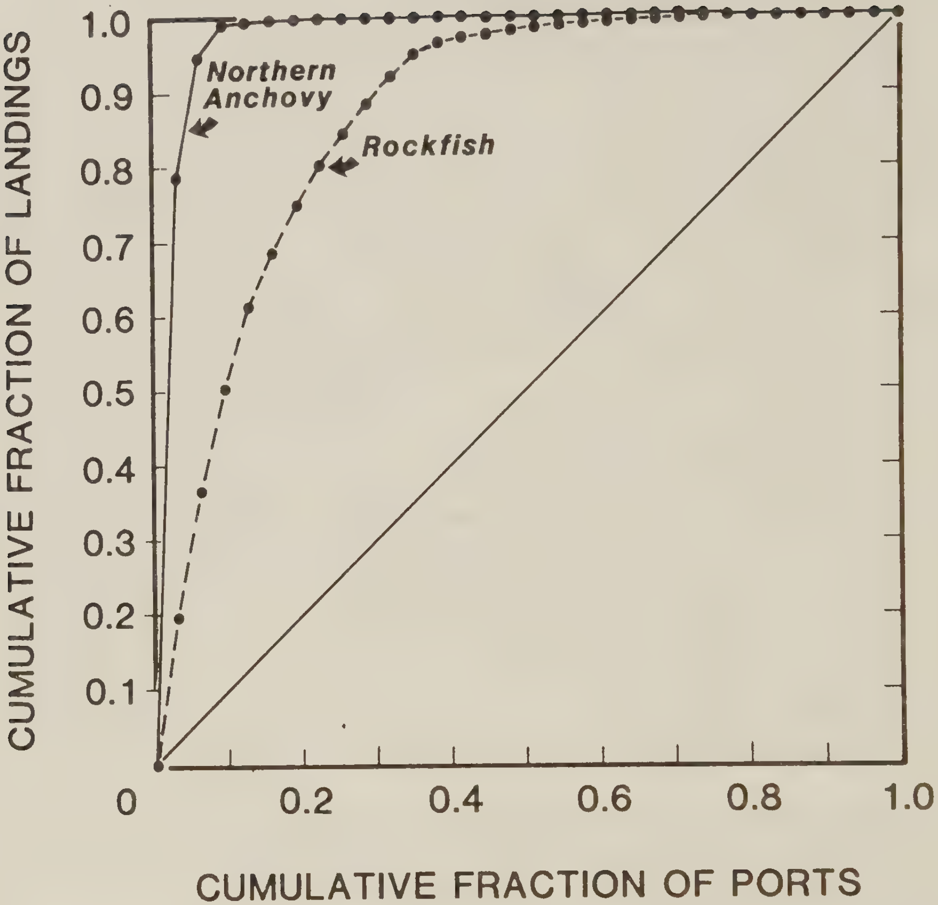

Figure 6. Comparison of relative geographic dispersion of landings of a pelagic fish (northern anchovy) and a groundfish species complex (rockfish, *Sebastes* spp.) in California in 1975.

Peru have reflected changes in abundance of pelagic fishes (Crawford and Shelton 1978). Monitoring of penguins and pinnipeds in the Antarctic has been proposed as a source of information on the abundance of forage species, including krill. Inexpensive (relative to the cost of seagoing surveys) monitoring of these "indicator species" could provide information, albeit imprecise, on changes in forage populations including a variety of forage species such as squids which have not been sampled effectively by existing methods.

Drawbacks to the use of indicator species include the difficulty of interpreting the information without verification or calibration. Use of indicator species as as a source of information for fishery management is unlikely not only because of imprecision, but because of the reluctance of fishermen to allow their fishery harvests to be governed by the performance of a competitor. In contrast, indicator

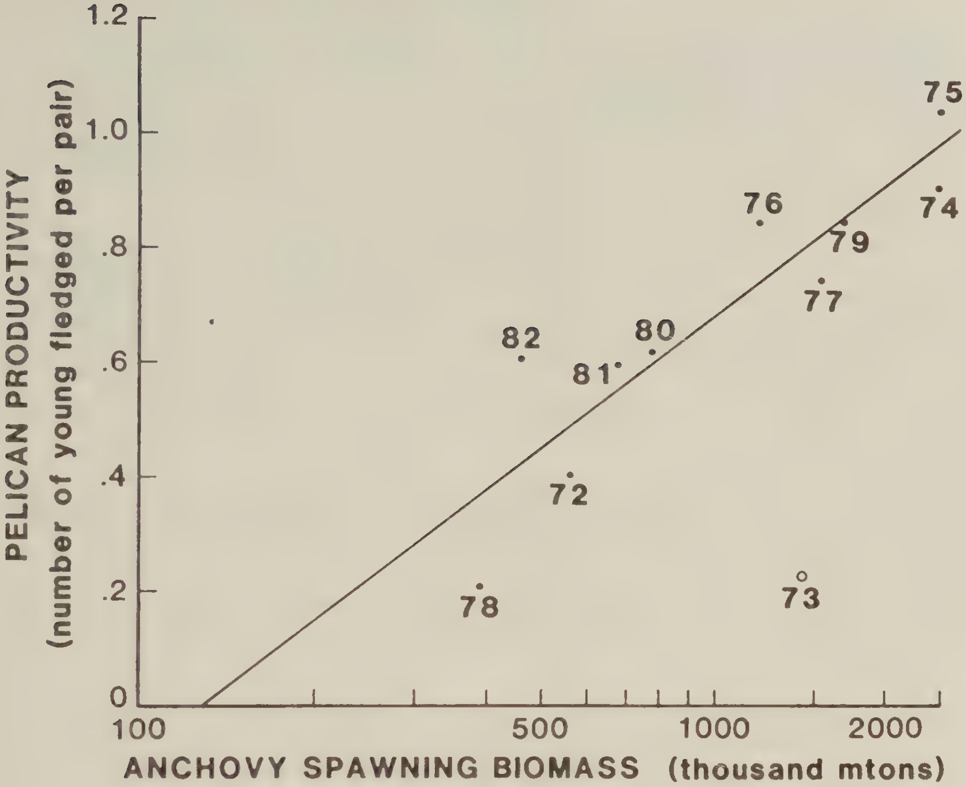

Figure 7. Relation between brown pelican productivity and anchovy spawning biomass off southern California (from MacCall et al. 1983).

species could be used quite effectively in the "low-information" management I described earlier.

WHO WILL DO THE WORK?

Fishery and ecosystem research is costly in time, money and manpower. For this reason alone, we must expect severe limitations on the amount of research which can be accomplished. There are additional barriers and impediments which render the work even more difficult. Areas of ecosystem research are divided into a bewildering number of jurisdictions and funding sources, with no single entity being responsible for coordination or integration. Further difficulties arise in large ecosystems which span international boundaries, where various nations may have very different policies toward research and management. The best hope for ecosystem research may lie in formation of consortia similar to CalCOFI on the Pacific coast (Baxter 1982, Reid 1982) which unite local, federal and perhaps international government agencies with academic institutions in pursuing and coordinating ecosystem studies. In the absence of incompatible goals (as might arise from implementation of the MMPA or the MFCMA) the mutual benefits should foster a strong and effective cooperative effort.

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8662

REVIEW OF THE BIOLOGICAL RATIONALE FOR IDENTIFYING SUBPOPULATIONS IN FISHERIES

ALEC MAC CALL
Southwest Fisheries Center, National Marine Fisheries Service

In looking through the literature for definitions of "stock," I felt that what I read did not address the subject very well. There are two important questions we have to answer in defining a stock. First, what do we want to use the definition for? I call this the operational consideration. The second question is, what do we know about the presumed stock? This is the informational consideration.

Often the first, or operational, consideration is the main one. If we consider the operational question exclusively, we can wind up with some biologically inappropriate, but nonetheless functional, stock definitions. For example, consider Ecuador's management of tuna in its territorial sea. Although the fish come and go from that area, the Ecuadoran government believes that this tuna is its stock, to manage however it wants. So Ecuador's definition of "stock" is purely operational and has very little biological basis. Similarly, an operational definition sometimes is necessary simply because of lack of knowledge. A good example comes from the multispecies trawl fishery in the Gulf of Thailand where a single trawl may bring up several dozen different species simultaneously, making it difficult to manage any single species. Several years ago during his work on this trawl fishery, John Gulland calculated the catch per effort and determined a production curve for all the species lumped together. Although people said, "You can't do that," his solution was, as a matter of fact, probably the best that could be achieved, and it did give an answer. His technique did relate the abundance and the productivity of the stock (in this case, made up of many species) to the rate of fishing.

These are extreme cases; we hope that most often there will be a balance between the operational and the informational components in the definition of a stock. I think some of the uncertainty about the utility of the stock concept has been the result of overlooking the first question. If we only look at biological considerations in an abstract case, we might formulate definitions of stock that have no use in the real world of management. My definition of stock is a modified version of Peter Larkin's definition[1] in which the operational and informational considerations are well-balanced. Stock is a population of organisms, [ideally] sharing a common gene pool, that is *sufficiently* discrete [and nominally identifiable] to warrant consideration as a self-perpetuating system that can be managed. (Emphasis and inserts are mine.)

I believe that all fishery management is based implicitly on the concept of a stock. The stock simply is that entity from which the catches are taken, and the problems of definition often reduce to a question of appropriate geographic scale. In many fisheries, the stock is simply defined by the method used to assess it. For example, virtual population analysis, sometimes called cohort analysis, defines the historical abundance of a stock simply by adding up the catches that were taken from it, with correction for mortality and other variables. There is a problem in deciding which catches to include, but, nonetheless, the method defines the stock. Similarly, in production modeling we plot the abundance in the form of a catch per unit effort against the effort. Presumably, the abundance declines as the rate of removal increases. In doing a production model, the question again is whether to put geographically dispersed populations together or to keep them separate. Perhaps the key is whether reproduction by one segment contributes to recruitment to the other segment. One way to answer that kind of question is to do a tagging study and see if the fishes actually move. Again, we wind up with a concept of a *de facto* stock, because the stock is simply defined by where the tags go. This leads to a fairly typical problem though: we have fuzzy edges.

I can demonstrate the nature of fuzzy edges from a tagging study of Pacific mackerel conducted from 1939 to 1941. There were five regions: Monterey Bay, southern California, northern Baja California, Sebastian Vizcaino Bay, and southern Baja. Quite a few tags were released in all of those locations—32,000 in southern California. We plotted the per thousand tags returned from various areas by the two major areas of release, southern California and central California.[2] In southern California we got 28 per thousand tags back, so that was designated unity, to which all the other areas' results were scaled. In northern Baja California, we got only 72% of unity back; in Sebastian Vizcaino Bay, 47%; and in southern Baja California, only 25%. As distance increased, the fraction of tags we got back decreased, but there isn't any place where the tagged fish just disappeared. This points up a continuing problem in stock definition; stocks slowly trail off with distance.

Although such tagging studies provide useful information about fisheries, they are very expensive because the researcher has to go to where the fish are. What we really prefer is some sort of simple, natural tag—an obvious morphological characteristic—so that we can bring the fish to us and figure out which ones they are. Such "tags" do exist, but are often concealed by natural variability among stocks or subpopulations. For example, off New Zealand, some scientists thought there might be two species of *Trachurus*, while others believed there was only one. The taxonomy was completely confused until about ten years ago when R. W. Gauldie used electrophoresis to demonstrate that there were two distinct electrophoretic patterns. This pattern was used to separate these fish into two groups, which then were seen clearly to differ morphologically. The position of the termination of the accessory lateral line differed considerably between the two species, although up to that time this was seen simply as a variable characteristic.[3]

To use a natural tag we must know enough about a species to identify an appropriate, variable characteristic. Often we have little knowledge about subpopulations or species, and about all we can do is to look at different geographic areas—let geography do the separating in a sense. For example, a study of the northern anchovy revealed that its length at a specified age is really quite variable in different areas along the Pacific coast, with variations of about one standard error. This difference is fairly direct evidence that mixing is limited. We do not know whether this is a genetic or an environmental characteristic, but once the fish are past a very small stage, their growth apparently is determined and they are not mixing.

In another study of anchovies, Jerry Spratt of the California Department of Fish and Game noticed that the size of anchovy otoliths relative to the size of the fish seemed to vary up and down the coast.[4] He compared otolith weight to fish length for various areas and found that, although for the very smallest fish there was no difference, as the fish got larger, the difference in otolith weight to fish length between the two groups was 1.5 standard errors apart, which is quite a solid difference. He projected that, based on that characteristic alone, there is about an 80% chance of categorizing a fish into the right group. Again, this strongly suggests that mixing is limited.

Based on tagging studies that showed that some fish actually do travel long distances along the coast, we originally had assumed that the population of anchovies was fairly thoroughly mixed. However, more recent evidence from the studies on length at age and other specific characteristics indicates that the fish in one geographic area are not mixing into other areas. Perhaps the whole population moves up and down to some extent, but there is limited mixing as far as we can tell.

In the case of major coastal pelagic fisheries, such as anchovies, sardines, and Pacific mackerel, the operational considerations are quite important, and for that reason we define our stock by fixed geographic boundaries. These boundaries are well defined operationally, and are particularly suited to fishery independent surveys, such as acoustic surveys, or egg and larvae surveys. The location of those geographic boundaries is based on genetic work done 10 to 20 years ago that indicated that there was a fairly sudden shift in the genetic composition in those areas. The work was limited, however, and we need to know more. One of the most difficult problems with a fixed geographic boundary is that the fish do move north and south seasonally; during oceanic anomalies such as El Niño, the movements are even stronger. Certainly the fish are not respecting our boundary. We do not know how much they move because we do not have good morphological characteristics by which to identify these stocks. In addition, even if the stocks are genetically distinct, they still may mix physically, so that in the vicinity of our boundary we may be able to catch either stock. We might know that two stocks are separate, but we cannot say where the separation occurs.

The boundaries, or clines, can be very strongly affected by fishing pressure, causing general shifts simply as a result of differential removals on one side of the boundary. A good example is the sardine fishery in which there was continuous northward migration of sardines all during the 1950s; as fishing removed sardines from southern California, they seemed to be steadily replaced by fish moving up the Baja California coastline.[5] We had reason to believe from blood serological research that there was a northern and a southern stock of sardines.[6] However, because fishing steadily removed the northern stock and there was a continual influx of southern stock, we may have totally annihilated the northern stock. Now there is a possibility of a resurgence of the sardine; we have evidence that the population is increasing. For a person like me who is going to have to write a management plan for this fish, it is rather important to determine whether the northern stock still exists. Is the new sardine stock going to be the same as the old or is it going to be something different? If the genetic composition is different, can we expect the productivity to be the same as for the old stock? If it looks as if it is the same stock as it used to be, we would feel more confident that the productivity would be the same. On the other hand, we might want to be more conservative if we see that the genetic composition is actually different than it used to be. Presumably, fish from the south are not as well adapted to reproducing in the colder waters to the north.

In the case of the sardine fishery, as in many cases in the United States, the answer to the first question I posed, "What do we want to use it for?" is clear. The Fishery Conservation and Management Act tells us that we are to manage these fisheries for optimum yield. The major problem is question number two, "What do we know about it?" Our ability to answer that question is limited by politics, money, and all of the usual constraints of scientific research.

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8663

Primary and secondary stress responses of striped bass (*Morone saxatilis*) exposed to benzene

R. B. MacFarlane and P. E. Benville, Jr.

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Center; Tiburon, California 94920, USA

Abstract

Striped bass (*Morone saxatilis*) were collected from the San Francisco Bay-Delta estuary in 1982, from areas distant from pollution sources. After acclimatization, plasma cortisol concentration (primary response) and blood biochemicals indicative of energy mobilization (secondary responses) were followed in individuals exposed to sublethal levels of benzene for up to 21 d. Despite the persistence of benzene in blood and liver tissues for the exposure duration, stress responses were moderate and returned to control values within the initial 7 d. Blood and liver rapidly accumulated benzene to approximately 20 times the exposure concentrations (0.1 and 1.0 ppm). Concentrations of cortisol and secondary response variables were not proportional to benzene exposure or to accumulation levels, however. Plasma cortisol concentrations increased two- to three-fold at 8 h and returned to control levels prior to 48 h exposure. Glucose, lactate, H^+, protein and triglyceride concentrations were elevated during the initial 4 h to 7 d, with protein and triglyceride returning to normal levels prior to the other secondary response variables. From the perspective of the general adaptation syndrome (GAS), benzene activated the hypothalamo-pituitary-interrenal axis, resulting in clinical stress responses characteristic of an alarm reaction. The time-courses and amplitudes of primary and secondary responses to benzene suggest the sensory perception of a noxious agent eliciting mild, acute stress followed by adaptation.

Introduction

The striped bass (*Morone saxatilis*) population of the San Francisco Bay-Sacramento River and San Joaquin River Delta estuary has declined by approximately 75% since the early 1960's (Stevens *et al.*, 1985). This decline has been attributed to any or all of four factors: reduced egg production, inadequate food supply for young striped bass, entrainment losses by water diversions, and pollution (Kelley, 1982). Studies have found high concentrations of organochlorines, metals and petrochemicals in striped bass tissues (Gadbois and Maney, 1983; Whipple *et al.*, 1983). Two-thirds of the striped bass sampled in 1978 contained benzene, a little-studied toxic aquatic contaminant, in liver tissue to approximately 4 ppm (Whipple *et al.*, 1983). These fish were in relatively poor physiological and reproductive condition, were heavily parasitized and exhibited a unique immune response to parasite infestations. In the most severe cases, this response was characterized by open external lesions which exposed internal organs (Moser *et al.*, 1985).

It is well established that fish exhibit characteristics of the general adaptation syndrome (GAS) (Selye, 1950) in response to a variety of stressors including many pollutants (Donaldson, 1981). The initial or alarm phase of the GAS is characterized by elevated plasma levels of corticosteroids and catecholamines which mediate secondary metabolic and physiological responses. These responses include mobilization and catabolism of lipids, proteins, and carbohydrates (Mazeaud *et al.*, 1977). Metabolic alterations have evolved as adaptive mechanisms to provide physiological compensation during suboptimal conditions. If adaptation occurs during continuous or repeated stressful conditions, homeostasis is regained and circulating levels of the "stress" hormones return to normal. However, if adaptation does not occur, the organism progresses into the exhaustion stage of the GAS, producing deleterious consequences such as reduced growth, reproductive impairment, immunological dysfunctions and, ultimately, death.

The purpose of the present investigation was to determine whether benzene exposure produces alterations of plasma cortisol, a primary stress response, and blood biochemicals indicative of energy mobilization in striped bass. Energy mobilization and metabolic effects of benzene exposure were evaluated by measuring circulating levels of glucose, lactate, H^+, triglycerides, and protein which have been shown to be responsive to stressors (Mazeaud and Mazeaud, 1981; Wedemeyer and McLeay, 1981).

Materials and methods

Morone saxatilis (2.9±0.6 yr old; 36.9±5.4 cm standard length; 944±342 g wet weight) were obtained by gill net and trawl from areas of the San Francisco Bay-Delta estuary distant from point sources of pollutants and were held in the laboratory for one to six months to acclimatize and eliminate any contaminants accumulated in the environment susceptible to depuration. The physiological condition of the experimental fish was assessed according to the procedures of Whipple *et al.* (1984) and was found to be representative of the healthier end of the spectrum in the Bay-Delta population, providing suitable subjects upon which to evaluate the effects of benzene exposure.

Striped bass were held in a 20 000-liter fiberglass raceway receiving filtered bay water (approximately 25‰ S and 15 °C) under ambient light conditions until 2 wk prior to experimentation (September, 1982), when they were transferred to the experimental tanks. Ten fish were randomly assigned to each of nine 2 200-liter circular fiberglass aquaria and acclimatized to filtered bay water flowing at a rate of 7 liters min^{-1} (27.5±1.7‰ S, 17.1 °C± 1.3 C°). Photoperiod in the experimental tanks was adjusted weekly to the natural cycle. Each tank was partially covered to minimize disturbance. Water quality measurements and behavioral observations were made daily throughout the acclimatization and experimentation periods. Dissolved oxygen was monitored with a calibrated YSI Model 54 oxygen meter (Yellow Springs Instrument Co., Yellow Springs, Ohio, USA) and had a mean value of 7.3±0.5 ppm. Unionized ammonia was measured at < 0.002 ppm by an Orion Model 95-10 ammonia electrode (Orion Research Inc., Cambridge, Massachusetts) corrected for temperature and pH. Fish were fed chopped squid twice weekly until satiated during acclimatization and experimentation, but never within 72 h of sampling to limit any possible contribution of feeding schedule to cortisol level (Delahunty *et al.*, 1978). There were no mortalities during either period.

Three of the experimental aquaria received water with a benzene concentration of 0.1 ppm (volumetric) calculated to produce liver benzene levels similar to those of striped bass collected from the San Francisco Bay-Delta. An additional three aquaria received water with a 1.0 ppm benzene concentration to amplify biological responses. Finally, three control aquaria received no benzene. Although rarely measured in the aquatic environment because of sampling and analytical difficulties, benzene is the most abundant aromatic hydrocarbon in the water-soluble fraction of certain crude oils (Anderson *et al.*, 1974), a major component of gasoline (Cornish, 1980), and has a solubility of 1 400 $\mu l\ l^{-1}$ in 25‰ S seawater at 16 °C (Benville and Korn, 1977). Based on data from the literature (Korn *et al.*, 1977; Whipple *et al.*, 1981), we believe 0.1 ppm to be a high environmental concentration. Within the proximity of a gasoline or petroleum spill, levels could equal or exceed 1.0 ppm (Hirsch *et al.*, in press). Both exposure concentrations were well below the 96 h LC_{50} (the concentration lethal to 50% of the test subjects within a specified time period) of 10.9 ppm for striped bass in a continuous-flow system (Meyerhoff, 1975). Initial benzene concentrations were rapidly produced by adding an appropriate volume of stirred, saturated benzene in distilled water stock solution (1 900 $\mu l\ l^{-1}$) to each aquarium. Concentrations were maintained by metering the benzene solution through Teflon tubing into the line delivering bay water to each tank. Benzene concentrations were determined twice daily using a Hewlett-Packard 5880 gas chromatograph (Hewlett-Packard, Avondale, Pennsylvania, USA) (Benville *et al.*, 1981). Charcoal filters were fitted to aquaria effluent lines to remove benzene.

Striped bass were exposed to benzene for 4 to 504 h (21 d). At each sampling time, one fish was removed from each tank to reduce capture-induced stress responses in other fish due to disturbances (as evidenced in brown trout by Pickering *et al.*, 1982). Within 2 min of initial disturbance, blood was withdrawn from each fish by cardiac puncture into Vacutainers (Becton Dickinson, Rutherford, New Jersey, USA) with and without heparin. One ml whole blood was immediately pipetted into 0.5 ml TF Freon, capped, and shaken vigorously for subsequent benzene analysis. Blood benzene concentrations were measured by injecting 3.2 μl of the Freon layer into the gas chromatograph using nonane as an internal standard. Samples for whole-blood lactate determination were prepared by pipetting 0.3 ml blood into 0.6 ml of 8% perchloric acid (weight/volume) at 4 °C and analyzed within 24 h according to the instructions supplied with the Sigma lactic acid test kit (Sigma Chemical Co., St. Louis, Missouri, USA). The pH of the blood was measured, followed by plasma isolation by centrifugation at 1 600×*g* for 10 min. Portions of plasma were then stored at –85 °C for subsequent glucose and triglyceride analyses. The remaining plasma was extracted for corticosteroid determination using C_{18} Sep-Pak cartridges according to the procedure of MacFarlane (1984), and stored at –20 °C. Serum separated from unheparinized blood samples was stored at –20 °C for protein analysis.

After blood collection, liver was excised and analyzed for benzene as described by Whipple *et al.* (1978). Corticosteroids were eluted from the Sep-Pak cartridges and determined by high-performance liquid chromatography (MacFarlane, 1984). Plasma glucose was measured by the hexokinase/glucose-6-phosphate dehydrogenase method using the Sigma test kit. Plasma triglyceride determination was accomplished by the enzymatic method of Bucolo and David (1973), which measures glycerol liberated by lipase hydrolysis, ultimately coupled to the oxidation of NADH.

The Lowry method was used for total serum protein determination (Lowry *et al.*, 1951). Statistical analysis of the data to evaluate the effects of benzene concentration and exposure time was performed by a fixed-effect, two-way analysis of variance (ANOVA) and covariance and by Duncan's multiple range test (Duncan, 1955) at significance levels of 0.10, 0.05 and 0.01 using SPSS statistical analysis computer programs (Nie *et al.*, 1975).

Results

Considering the volatility of benzene, the dosing system provided stable concentrations in the aquaria (Fig. 1). All tanks attained benzene concentrations within 10% of the targeted values within 1 h of benzene addition. The mean benzene concentrations for the 21 d experimental duration were 0.113 ± 0.006 ppm and 1.008 ± 0.148 ppm for the low and high exposures, respectively. The only difficulty occurred between 7 and 14 d exposure when, in two of the high-exposure tanks, a benzene-consuming microbial (presumably bacterial) growth developed and reduced the concentration. This was corrected by spiking the tanks with the appropriate volume of a saturated benzene solution via a siphon placed beside the inflowing water until the desired concentration was regained. During this period, dissolved oxygen declined to 5.0 ppm but no signs of respiratory distress in *Morone saxatilis* were observed.

Benzene concentrations in blood revealed rapid uptake, attaining maximal levels by 8 h in the low exposure and 24 h in the high exposure (Fig. 1). The variability of benzene concentrations in blood among fish at each exposure level and sampling time was low. However, the decline of benzene in tanks with microbial blooms resulted in significant decreases in blood benzene concentrations in fish at 7 and 14 d. Regression of blood benzene level at the time of sacrifice on the water benzene level for all exposed fish revealed that blood concentrates benzene to a steady state of approximately 20 times the water concentration ($[\text{benzene}_{\text{blood}}] = 0.13 + 19.93\ [\text{benzene}_{\text{water}}]$, $r = 0.96$, $n = 42$).

Liver accumulated high concentrations of benzene (Fig. 2). Exposure to 0.1 ppm benzene achieved tissue levels within the range observed in livers of field specimens of Bay-Delta striped bass. Similar to blood, uptake was rapid and maximum concentrations were attained sooner in the low-exposure than in the high-exposure tanks. The decline of liver benzene in the 1.0 ppm exposure followed the declines of benzene in the water and blood. Regression analysis revealed that benzene concentrations in liver were essentially the same as in blood for all exposure durations ($[\text{benzene}_{\text{liver}}] = 0.23 + 0.93\ [\text{benzene}_{\text{blood}}]$, $r = 0.90$, $n = 42$). This relationship indicates that the liver does not accumulate unmetabolized benzene above the concentration found in blood. Within the exposure duration to the benzene concentrations tested,

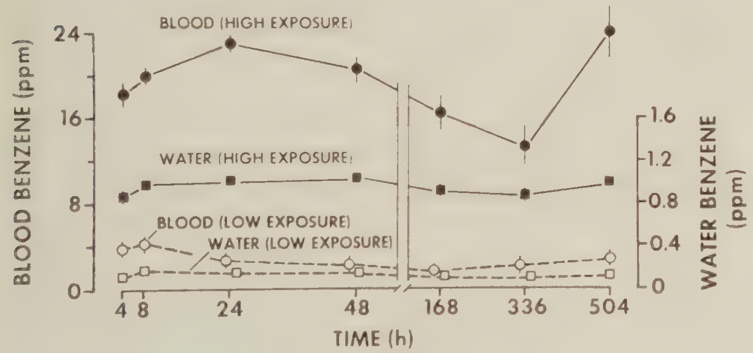

Fig. 1. *Morone saxatilis.* Benzene concentrations in exposure tanks and blood. Targeted benzene concentrations in water were 0.1 and 1.0 ppm for low and high exposures, respectively. Values represent means ± SE; where error bars are not shown, SE was less than size of symbol

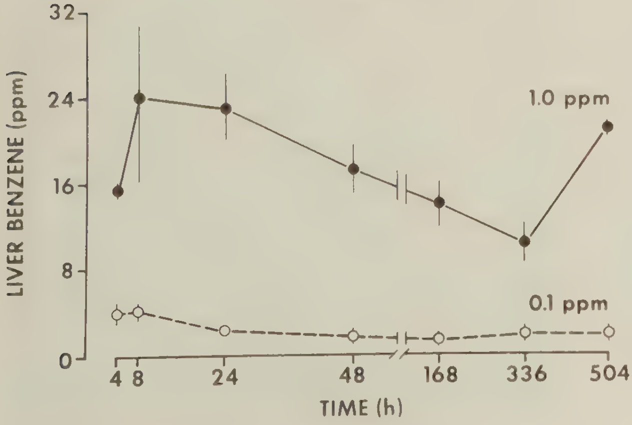

Fig. 2. *Morone saxatilis.* Accumulation of benzene in liver. Targeted benzene-exposure concentrations are indicated. Values represent means ± SE

Table 1. *Morone saxatilis.* Results of a fixed-effect, two-way analysis of variance for changes in blood variables at three levels of benzene exposure (0, 0.1 and 1.0 ppm) for seven exposure durations up to 504 h; DF: degrees of freedom; MS: mean square

Variable	Source	DF	MS	*F* ratio
Cortisol	Main effects	8	4 203.00	8.92**
	[benzene]	2	1 972.36	4.18*
	time	6	4 947.70	10.50**
	Two-way interaction	12	3 298.13	7.00**
	Residual	41	471.37	
	Total	62	1 570.07	
Glucose	Main effects	8	2.19	11.31**
	[benzene]	2	5.03	25.97**
	Time	6	1.25	6.45**
	Two-way interaction	12	0.42	2.14*
	Residual	41	0.19	
	Total	62	0.52	
Lactate	Main effects	8	0.94	16.21**
	[benzene]	2	2.19	37.61**
	time	6	0.52	8.95**
	Two-way interaction	12	0.11	1.89
	Residual	41	0.06	
	Total	62	0.18	
pH	Main effects	8	0.05	17.79**
	[benzene]	2	0.09	35.26**
	time	6	0.03	11.75**
	Two-way interaction	12	0.003	1.16
	Residual	41	0.003	
	Total	62	0.008	
Protein	Main effects	8	0.89	6.03**
	[benzene]	2	2.19	14.82**
	time	6	0.46	3.08*
	Two-way interaction	12	0.29	1.97
	Residual	41	0.15	
	Total	62	0.32	
Triglyceride	Main effects	8	44 034.35	7.71**
	[benzene]	2	27 075.27	4.74*
	time	6	49 164.79	8.60**
	Two-way interaction	12	10 321.42	1.81
	Residual	41	5 714.97	
	Total	62	11 726.79	

* $P<0.05$; * $P<0.001$

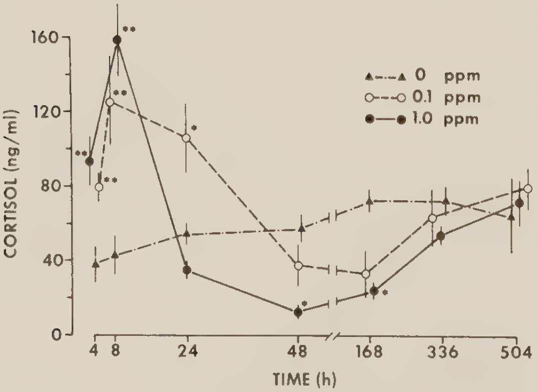

Fig. 3. *Morone saxatilis.* Plasma cortisol concentrations in benzene-exposed and control striped bass. Values represent means ±SE. Asterisks denote values significantly different from same-time control values (Duncan's multiple range test: * $P<0.05$; ** $P<0.01$)

the concentration of benzene in the blood was a linear function of benzene level in the water and benzene in the liver was a linear function of blood benzene-level.

Cortisol was the only corticosteroid detected in the plasma of the striped bass. Both benzene concentrations produced elevated cortisol levels within 4 h of exposure and maximal responses at 8 h (Fig. 3). Cortisol responses to both benzene levels at 4 and 8 h were similar and were not proportional to exposure concentrations. Cortisol declined after 8 h, with a greater decline in the 1.0 ppm exposure. Control cortisol levels were attained by 24 h in 1.0 ppm benzene, but were not achieved until 48 h in the 0.1 ppm concentration. Analysis of variance revealed a significant interactive effect of benzene on plasma cortisol ($P<0.001$) (Table 1). Comparison of benzene-exposed fish with same-time controls by Duncan's multiple range test revealed that cortisol concentrations were significantly greater in fish exposed to both benzene levels at 4 and 8 h

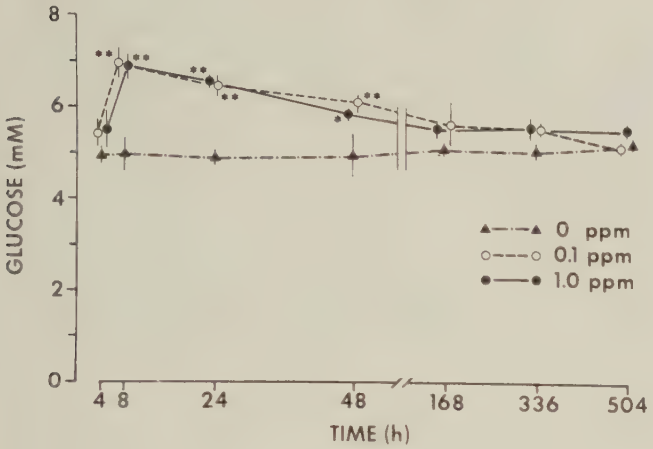

Fig. 4. *Morone saxatilis.* Plasma glucose concentrations in benzene-exposed and control striped bass. Further details as in Fig. 3

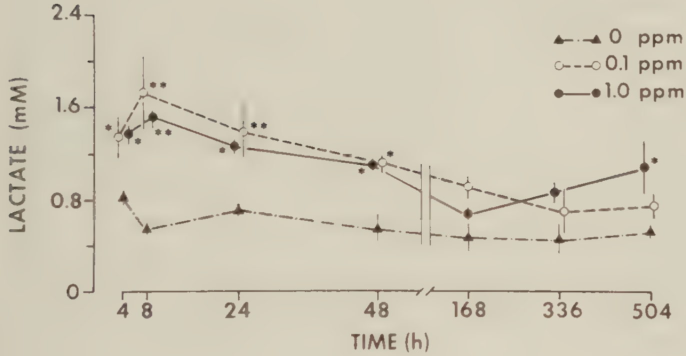

Fig. 5. *Morone saxatilis.* Blood lactate concentrations in benzene-exposed and control striped bass. Further details as in Fig. 3

($P < 0.01$) and at 24 h in the 0.1 ppm benzene exposure ($P < 0.05$). Cortisol concentrations were significantly lower, however, at 48 h and 7 d in 1.0 ppm benzene ($P < 0.05$) compared to same-time controls. At the 0.05 significance level, mean cortisol values of controls at all sampling times were not significantly different.

Elevated plasma glucose developed later and persisted longer than the cortisol response in both benzene concentrations (Fig. 4). Hyperglycemia was not evident until 8 h exposure and control values were not re-established until after 48 h. Responses were essentially identical for both exposure concentrations, with maximal concentrations recorded at the same sampling time as for cortisol. Analysis of variance showed a significant interactive effect of benzene level and exposure time on plasma glucose ($P < 0.05$) (Table 1). Exposure to both benzene concentrations resulted in significant glucose elevations compared to control values at 8, 24, and 48 h.

Blood lactate concentrations were significantly elevated for the first 48 h in fish exposed to both benzene levels (Fig. 5). The time-course of the response was similar to that of glucose and was not dose-dependent. However, unlike glucose, lactate was significantly greater at 4 h exposure compared to controls, and there was a secondary elevation at 21 d exposure to 1.0 ppm benzene. Both main effects were statistically significant ($P < 0.001$) (Table 1).

Striped bass exposed to benzene exhibited lower blood pH than controls (Fig. 6). The greatest depressions of blood pH occurred during the first 8 h in both treatments and returned to control values by 7 d exposure. However, there was a secondary pH decrease in the 1.0 ppm benzene exposure by 14 d that corresponded to increasing lactate. ANOVA revealed significant individual main effects of benzene concentration and exposure time ($P < 0.001$) similar to lactate (Table 1). The association between blood lactate and pH observed in these experiments indicated metabolic acidosis and is supported by the correlation of H^+ and lactate concentration, $r = 0.88$, $n = 42$, $P < 0.001$.

Benzene exposure produced a moderate elevation in serum protein (Fig. 7). Protein was maximal at 4 h exposure to 1.0 ppm benzene and at 8 h in 0.1 ppm media. Control levels were established by 24 to 48 h with no further responses evident for the duration of the exposures. ANOVA revealed significant individual main effects of benzene concentration and exposure duration (Table 1).

Plasma triglyceride responded rapidly to benzene exposure, attaining approximately 550 mg dl^{-1} at 4 h, but

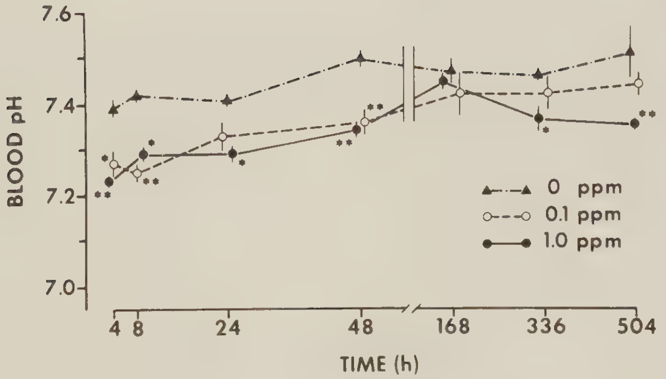

Fig. 6. *Morone saxatilis.* Blood pH in benzene-exposed and control striped bass. Further details as in Fig. 3

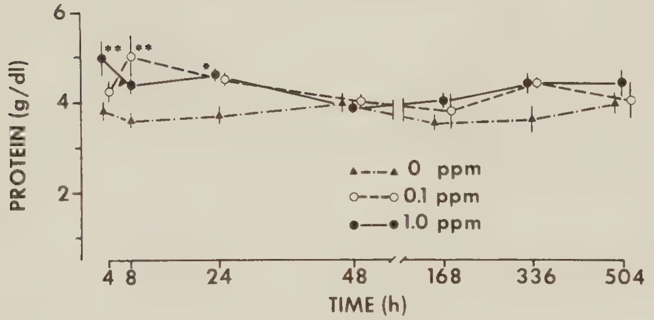

Fig. 7. *Morone saxatilis.* Serum protein concentrations in benzene-exposed and control striped bass. Further details as in Fig. 3

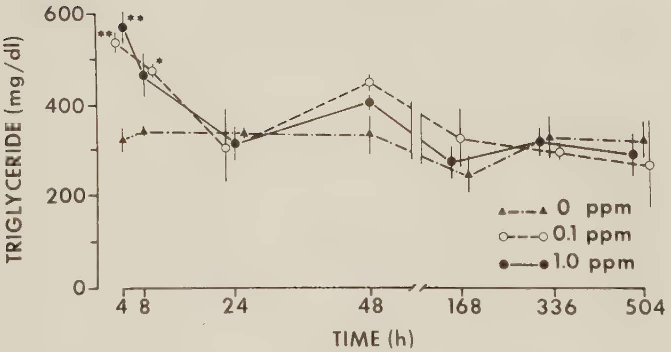

Fig. 8. *Morone saxatilis.* Plasma triglyceride concentrations in benzene-exposed and control striped bass. Further details as in Fig. 3

rapidly declined to control levels within 24 h (Fig. 8). Similar to the other biochemical responses, plasma triglyceride was not dose-dependent; both benzene concentrations evoked similar elevations and time-courses.

Alterations in behavior were observed in striped bass exposed to benzene. During the initial 4 d, exposed fish swam more continuously, appeared much more restless and displayed greater frequency and amplitude of opercular movements than controls. These responses were greater in the 1.0 ppm benzene solution than in the lower concentration. From Day 4 through Day 7, exposed striped bass performance was more similar to that of controls. After 7 d, fish in benzene-dosed water became increasingly hyperactive, particularly in the high benzene exposure.

Feeding was on a random schedule to eliminate food-induced effects on blood variables and was never within 3 d prior to sampling. Fish exposed to both benzene concentrations ate well when food was presented on Day 2 after sampling. After 7 d exposure, those in 1.0 ppm benzene ate approximately 50% of the ration within 2 h of presentation. By 14 d exposure, only about 10% of the food was consumed. Striped bass in 0.1 ppm benzene consumed about 75% of the ration on Day 7 within 1 h of presentation; thereafter, they ate less than 50% of the ration over a several-hour period. In contrast, controls always consumed 100% of the ration within 10 to 30 min.

Discussion

The time-courses of the cortisol and secondary metabolic responses of *Morone saxatilis* to benzene exposure are characteristic of mild, acute stress elicited by the sensory perception of a noxious agent. These responses, typical of the alarm phase of the general adaptation syndrome (Selye, 1950), were followed by a return to control levels within 2 to 7 d despite the persistence of benzene in blood and liver for the 21 d duration of exposure. Thus, the resistance phase of the GAS had occurred. These results are congruous with the concept discussed by Schreck (1981) that the initial moments during encounter with a stressor that causes fright, pain or discomfort are the most important in establishing clinical stress responses. This phenomenon has been observed with other fish challenged by chemical stressors (Schreck and Lorz, 1978; Thomas and Neff, 1985). Sensory perception of benzene is supported by the recent study of Babcock (in press). When exposed to sublethal concentrations of benzene, pink salmon (*Oncorhynchus gorbuscha*) olfactory rosettes contained exhausted mucous cells, indicating olfactory stimulation.

Uptake and equilibrium of benzene in the blood were rapid. The major uptake pathway for benzene appears to be across the gill membrane with subsequent sorption by blood cells and perhaps lipoproteins (Gerarde, 1960; Whipple *et al.*, 1981). Benzene removal from blood was in a steady state with liver uptake, as revealed by the relationship of benzene concentrations in blood and liver. Liver is a major site of benzene accumulation and metabolism in striped bass (Korn *et al.*, 1976; Whipple *et al.*, 1981) and other teleosts (Korn *et al.*, 1977; Roubal *et al.*, 1977). Liver benzene concentrations in fish exposed to 0.1 ppm were within the concentration range found in livers of striped bass obtained from the San Francisco Bay-Delta (0.02 to 4.02 ppm, $N = 105$, Whipple *et al.*, 1983), justifying this exposure concentration as a valid environmental level.

Rapid metabolism of benzene was suggested in the present study by the steady-state relationship between benzene concentrations in blood and liver and by the coincidental declines of benzene in water and liver during the microbial blooms. Radiolabelled tracer studies suggest that benzene is metabolized in hepatic tissue, stored in the gall bladder, and excreted in the feces and urine (Korn *et al.*, 1976, 1977; Roubal *et al.*, 1977). As in mammals, hepatic detoxification is probably accomplished by hydroxylation reactions by cytochrome P-450 and the mixed function oxygenase (MFO) system to form phenol, catechol and hydroquinone, followed by the formation of glucuronide and sulphate conjugates (Jerina and Daly, 1974; Snyder and Kocsis, 1975).

Activation of the hypothalamo-pituitary-interrenal axis had occurred prior to the first sampling at 4 h exposure to benzene. Plasma cortisol was elevated during the initial period of exposure but returned to control, or lower, values despite the continued presence of the stressor, as observed in other studies (Donaldson and Dye, 1975; Schreck and Lorz, 1978; Leach and Taylor, 1980; Thomas *et al.*, 1980, 1981; Tomasso *et al.*, 1981). From the perspective of the GAS, responses of this type suggest that the animal is in the process of adapting to an altered environment following a period of alarm. This is in contrast to the results of other studies where cortisol remained elevated throughout the duration of stressor exposure (DiMichele and Taylor, 1978; Barton *et al.*, 1980). The former pattern appears more common, suggesting that fish can generally adapt to mild, chronic stressors. Of course, this ability is influenced by many factors such as the type, duration and intensity of the stressor; the life stage; and the presence or absence of other stressing agents. Thomas *et al.* (1980) conjectured that volatile compounds including benzene, in addition to naphthalene, were involved in the acute elevation of plasma cortisol in *Mugil cephalus* exposed to a 20% water-soluble fraction of No. 2 fuel oil. The present study supports that conjecture. Due to the method of exposure, Thomas *et al.* (1980) were unable to establish whether adaptation of the cortisol response to aromatic hydrocarbons occurred. Cortisol titers in *Fundulus heteroclitus* after 15 d exposure to naphthalene suggested that adaptation did not occur (DiMichele and Taylor, 1978). Our study indicates adaptation does occur, at least in striped bass. Of course, longer exposure resulting in loss of adaptation and therefore exhaustion can not be excluded.

In striped bass exposed to 1.0 ppm benzene, the decline of cortisol to levels below those of controls could be attributed to several processes including interrenal exhaustion, feedback inhibition of ACTH production, or enhanced metabolism of cortisol. The first two possibilities are unlikely since the duration of the cortisol response was shorter than has been recorded from other studies (DiMichele and Taylor, 1978; Schreck and Lorz, 1978) and the amplitude of the cortisol response was much less than the response produced by confinement stress (MacFarlane, 1984). Enhanced hepatic metabolism of cortisol in benzene-exposed fish was more likely the cause of the decline. Although not evaluated in the present study, benzene induction of the mixed function oxygenase (MFO) system, known to occur in mammals (Snyder and Kocsis, 1975), may account for reduced plasma levels of cortisol. There is evidence that the same MFO system can metabolize both steroids and xenobiotics in birds and mammals (Kupfer and Peets, 1966; Conney, 1967; Nowicki and Norman, 1972) and that such stimulation of cortisol metabolism can result in depletion (Kupfer, 1975). Sivarajah *et al.* (1978) found a correlation between increased hepatic microsomal enzyme activity and decreased plasma steroids in *Cyprinus carpio* and *Salmo gairdneri* exposed to the PCB, Aroclor 1254. Induction of this detoxification mechanism is rapid. Lee *et al.* (1972) demonstrated that metabolism of naphthalene was essentially complete within 24 h of exposure in three species of marine fishes.

Elevated plasma corticosteroids and catecholamines promote an array of secondary metabolic responses to adapt an animal to an altered environment (Selye, 1950; Donaldson, 1981). In the present study, the time-courses of blood variables indicative of energy mobilization and utilization were consistent with the cortisol response and indicated initial, transitory stress followed by adaptation to benzene exposure within 7 d. During the alarm phase, responses to both benzene concentrations were essentially similar. Furthermore, hematological measurements (e.g. hematocrit, hemoglobin, etc.) revealed that plasma levels of blood biochemicals were not attributable to hemoconcentration. The effects of benzene on striped bass hematology will be the subject of a future paper (MacFarlane, unpublished data).

The rise in plasma glucose, often observed in teleosts in response to stressors (Silbergeld, 1974; Mazeaud *et al.*, 1977), succeeded the cortisol response and persisted for longer than 48 h. Since glucose mobilization is promoted by cortisol and catecholamines, this pattern is not unexpected and was similar, but of lower magnitude, to that seen in the mullet *Mugil cephalus* exposed to the water-soluble fraction of No. 2 fuel oil (Thomas *et al.*, 1980). Plasma glucose concentrations generally return to control levels within 4 d following acute forms of stress (Pickering *et al.*, 1982). Persistent elevations have been recorded, however, in some teleosts exposed to pollutants (Holmberg *et al.*, 1972; Grant and Mehrle, 1973).

Blood lactate can be elevated by stress or muscular activity which often accompanies stress (Love, 1980). Lactate elevation in benzene-exposed individuals preceded the glucose response and a secondary rise was observed by 21 d exposure to 1.0 ppm. Both periods co-occurred with moderately increased swimming activity and restless behavior, indicating that increased lactate was a result of hyperactivity and excitement. Prolonged blood lactate elevations following stress or exercise have been attributed to a catecholamine-mediated slow release from muscle (Wardle, 1978). In the present study, prolonged lactate elevations occurred, and were correlated with the depression of blood pH. A similar relationship has been observed in other fishes (Black, 1958; Cliff and Thurman, 1984). In some investigations, lower blood pH preceded increased lactate (Black *et al.*, 1959; Wood *et al.*, 1977) and has been attributed to respiratory acidosis. Delayed or prolonged decreases in blood pH are the result of metabolic acidosis (Wood *et al.*, 1983). The time-course of blood lactate levels and the correlation between lactate and pH observed in benzene-exposed striped bass suggest metabolic acidosis as a contributory source of increased H^+. The less than one-to-one stoichiometric relationship between lactate and hydrogen ions could be due to increased ventilation as a compensatory mechanism buffering the fall of pH (Hughes, 1981). Greater frequency and amplitude of opercular movement were observed in the present study in fish exposed to benzene during the first 4 d and after 7 d, corresponding to periods of high lactate and low pH. Increased oxygen consumption has been demonstrated in striped bass exposed to benzene (Brocksen and Bailey, 1973).

It is generally believed that mobilization of protein, promoted by corticosteroids, occurs in the form of free amino acids from peripheral tissues for gluconeogenesis and enzyme synthesis in liver (Bondy, 1980). Other studies of teleosts subjected to stressors have demonstrated increased protein levels in plasma and serum (Holmberg *et al.*, 1972; DiMichele and Taylor, 1978; Peters *et al.*, 1980; Brown *et al.*, 1984). Bouck (1972) suggested that protein was released into blood from tissues in the rock bass *Ambloplites rupestus* under hypoxic stress, and Silber and Porter (1953) demonstrated increased plasma albumin in rats treated with cortisone. Results of the present study indicate that benzene-induced stress activates protein metabolic sequences. Elevated levels of serum protein preceded increased plasma glucose in individuals exposed to 1.0 ppm benzene, supporting the contention of Walton and Cowey (1982) that fish utilize protein preferentially to glucose for energy production.

Stress promotes alterations in lipid metabolism and mobilization, although results of research with fish have not revealed a clear, consistent process (Love, 1980; Mazeaud and Mazeaud, 1981). The rapid increase and subsequent return to control values of plasma triglyceride in benzene-exposed striped bass is very similar to the response of blood free fatty acids in carp (*Cyprinus carpio*) following a single administration of epinephrine (Mazeaud *et al.*, 1977). This similarity indicates again that benzene exposure produces a transitory, acute alarm reaction to the perception of a noxious agent and does not evoke chronic GAS-type effects. Increased concentrations of plasma triglyceride have been reported in eels (*Anguilla anguilla*) and coho salmon (*Oncorhynchus kisutch*) exposed to 0.1 ppm pentachlorophenol (Hanes *et al.*, 1968; Holmberg *et al.*, 1972) and in mullet (*Mugil cephalus*) exposed to dibenzofuran (Thomas *et al.*, 1981). Unaltered, or decreased, triglyceride levels were found in mullet exposed to fluorene, carbazole, and dibenzothiophene, however. It appears that the variability of a triglyceride response is dependent on various factors, including the type of stressor and the relative importance of lipid as an energy source in a particular species. Lipid is a major fuel in striped bass, as reflected by relatively high concentrations in blood (1.5 to 3.5 g dl^{-1}), liver (5 to 20%) and muscle (2 to 9%) (Gadbois and Maney, 1983; MacFarlane, unpublished data).

In summary, exposure to benzene concentrations which produced tissue burdens equal to or greater than those found in striped bass in the San Francisco Bay-Delta estuary produced alterations in blood biomolecules characteristic of the GAS. Primary and secondary responses revealed a consistent pattern typical of mild, acute stress. These results indicated that striped bass responded to the sensory perception of a noxious stimulus by activation of the hypothalamo-pituitary-interrenal axis, and that the resistance, or adaptation, stage of the GAS was attained.

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RELATIVE ABUNDANCE OF FOUR SPECIES OF *SEBASTES* OFF CALIFORNIA AND BAJA CALIFORNIA

JOHN S. MacGREGOR
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

Estimates of relative abundance of rockfish larvae were made for the area from San Francisco to southern Baja California. Over the 14 years studied, 30% of spawning occurred in February, 18% in January, 17% in March, and 12% in April. For the four identified species of rockfish larvae, peak spawning occurred in February (65%) for *S. jordani*; in January (45% and 40%, respectively) for *S. levis* and *S. paucispinis*; and in April (32%) for *S. macdonaldi*.

Half of the *S. jordani* larvae were taken within 10 nautical miles of land. About half of the other three species were taken within 20 nautical miles of land. *Sebastes* larvae were most abundant off San Francisco and Monterey and in the area of the Channel Islands off southern California, with the former area accounting for 53% of all larvae and the latter for 35%.

RESUMEN

Se estimó la abundancia relativa de larvas de *Sebastes* en el área entre San Francisco y el Sur de Baja California. Durante los 14 años de estudio, un 30% del desove ocurrió en febrero, un 18% en enero, un 17% en marzo, y un 12% en abril. Para las cuatro especies de larvas de *Sebastes* identificadas, el desove máximo se presentó en febrero (65%) para *S. jordani*, en enero (45% y 40%, respectivamente) para *S. levis* y *S. paucispinis*, y en abril (32%) para *S. macdonaldi*.

La mitad del número de larvas de *S. jordani* fue colectada dentro de las 10 millas náuticas desde la costa. Alrededor de un 50% de las otras tres especies fue colectado dentro de las 20 millas náuticas desde la costa. Las larvas de *Sebastes* fueron más abundantes frente a San Francisco y Monterey (53% del total de larvas), y en el área de las "Channel Islands" al Sur de California (35%).

INTRODUCTION

Hubbs et al. (1979) list 62 species of rockfish of the genus *Sebastes* occurring in the coastal waters of California. Some rockfishes are important to sport and commercial fisheries; others are too infrequently taken or do not grow large enough to significantly contribute to the fisheries.

Since 1950, CalCOFI members the National Marine Fisheries Service (U.S. Department of Commerce), its predecessor agency the Bureau of Commercial Fisheries, and Scripps Institution of Oceanography have furnished vessels to obtain biological, physical, and chemical samples over a pattern of stations off the coasts of California and Baja California (see inside back cover). The pattern was sampled monthly for the ten years from 1950 through 1959 and has been sampled intermittently since then.

Plankton are sampled at each station with a 1-m net. The larval fish taken in each net tow are identified and enumerated. In past years rockfish were identified to genus only. More recently (1977) Moser et al. described the larvae of 4 of the 62 species—*S. paucispinis* (bocaccio), *S. jordani* (shortbelly rockfish), *S. levis* (cow rockfish), and *S. macdonaldi* (Mexican rockfish).

Ahlstrom (1959) obtained information on the temperature and depth distribution of larval rockfish from a series of 17 vertical distribution net tows at 12 depths from 2 to 285 m. *Sebastes* larvae were taken at temperatures between 9.0° and 17.2°C, with the larger concentrations occurring at temperatures between 10.2° and 16.1°. Ahlstrom found that only nine rockfish larvae were taken below 100 meters (actually in the 122-89-m haul). The depth distribution follows a normal distribution (Figure 1), with a peak at about 40 m and a standard deviation of 21.6 m. However, distribution is probably determined to a considerable extent by the position of the thermocline. Ahlstrom also decided that there was no significant difference between the numbers of rockfish larvae taken in night and day net hauls. (For some species of fishes more larvae are taken in night hauls.)

This paper presents data based on the identification and enumeration of the larvae of four species of rockfish for 5 CalCOFI survey years and for all *Sebastes* larvae for 14 years. Although it is not yet possible to identify all sizes of larvae of most rockfish species, the results of this study provide a background for evaluating the potential use of larval surveys to study distribution and abundance. The larval data were provided by H. Geoffrey Moser, under whose direction

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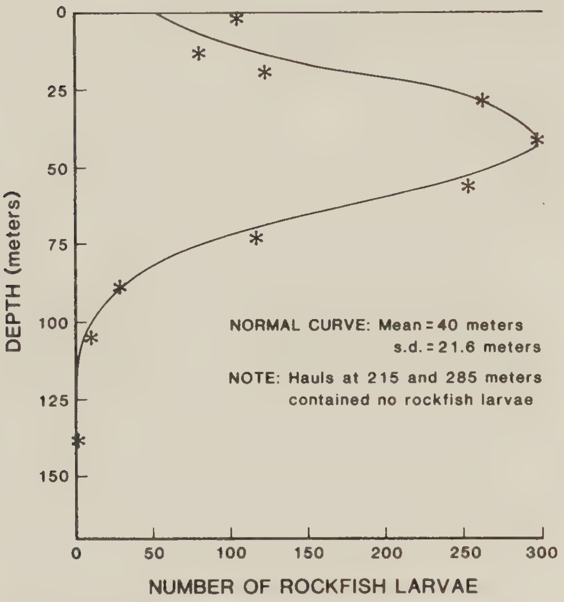

Figure 1. Depth distribution of rockfish larvae.

the four species of larval rockfishes were identified, counted, and measured by Elaine Sandknop with the assistance of Connie Fey and Susan D'Vincent.

MATERIALS AND METHODS

Sebastes larvae taken at each CalCOFI station for each survey cruise have been enumerated routinely each year. For this study, larvae of *S. paucispinis*, *S. jordani*, *S. levis*, and *S. macdonaldi* were identified, counted, and measured for each monthly survey for the years 1956, 1969, 1972, 1975; for *S. jordani* and *S. macdonaldi* 1966 was also included.

Routine CalCOFI plankton sampling methods and equipment have been described in detail by Ahlstrom (1948, 1953). The amount of water strained by the plankton net is measured so that the data may be converted to the numbers of organisms under one square meter of sea surface and therefore be comparable between stations.

The area included in this survey extended from the strip of ocean represented by CalCOFI line 60, just north of San Francisco Bay, to the strip represented by line 157, off the southern tip of Baja California (inside back cover). Coverage of the area north of line 60 was too spotty to be usable. The number of rockfish larvae taken at each station was expanded to give an abundance estimate for the area represented by that station. These estimates were combined to estimate the larval population present in the 40-nautical-mile-wide strip of ocean represented by each CalCOFI line. In some months no cruise was made, or some lines were omitted from the pattern. Estimates were calculated for these omissions based on the average percentages of larvae taken in those months or on those lines in the other years when they were sampled; i.e., if *X*% of the larvae were taken on a line or in a month when they were sampled, I assume that *X*% were present at similar times when they were not sampled. However, these omitted lines or months were generally outside the main spawning season and did not affect the estimates significantly. The estimates obtained are for the numbers of larvae in the area at the time of the cruise. No data are available that would allow us to interpolate between months in order to obtain more representative estimates of annual spawning.

Although the stations on some lines were sampled much farther to sea than on others, I believe that most of the offshore distribution was sampled adequately. Half of the *S. paucispinis* and *S. macdonaldi* larvae were taken within 20 nautical miles of land, and half of the *S. jordani* larvae within 10 nautical miles of land (Table 1). *S. paucispinis* appears to have a somewhat more offshore distribution than the other larvae, while the distribution of *S. jordani* is more inshore. There were too few data to determine the offshore distribution of *S. levis*, but it appears to be similar to the other *Sebastes* larvae.

The numbers and percentages in the tables include several degrees of magnitude. Digits are retained in the larger numbers for purposes of alignment and do not imply great accuracy of these numbers.

RESULTS AND DISCUSSION

Estimates of larval rockfish abundance in the area represented by lines 60 through 137 (Table 2) range from 38×10^{12} in 1959 to 219×10^{12} in 1969 for the 14 years 1950-59, 1966, 1969, 1972, and 1975. The 14-year average abundance is 135×10^{12} larvae.

Because rockfishes are live bearers whose larvae develop within the ovaries and hatch at the time of spawning, and because most of the larvae taken were close to the hatching size, the occurrence of larvae should delimit the spawning season fairly well. For the 14 years 18% of the spawning occurred in January, 30% in February, 17% in March, and 12% in April.

In any given year, if the spawning was low in one of these four months, it tended to be low in the other three months, and, if high, it tended to be high in the other three months. Rank correlation of the amount of spawning in January, February, and March yielded correlation coefficients of 0.65 (January/February), 0.70 (January/March), and 0.78 (February/March). The correlation coefficient for a probability of 0.01 is 0.66. Correlations with April were less significant.

TABLE 1
Cumulative Percentage Distribution of Rockfish Larvae (Five-Year Average) Relative to Distance from Nearest Land for Each of Three Species Compared to Percent Distribution of All Species of Rockfish Larvae Less the Species Compared

Nautical miles from land	*Sebastes paucispinis*	All other rockfish	*Sebastes jordani*	All other rockfish	*Sebastes macdonaldi*	All other rockfish
0-10	29.3	63.7	56.9	65.6	43.9	46.5
0-20	50.4	76.6	68.2	76.7	56.5	65.6
0-30	56.9	85.4	93.3	83.1	69.7	85.0
0-40	74.4	90.1	97.0	88.5	81.2	89.2
0-50	85.8	95.2	99.1	94.2	83.3	92.9
0-100	97.6	98.5	99.9	98.2	100.0	96.4
0-150	99.1	99.2	100.0	99.2		98.1
0-200	100.0	99.8		99.7		100.0
0-250		100.0		100.0		

Total rockfish larvae include only larvae occurring in the same areas as species with which compared; i.e., no *S. paucispinis* larvae were taken south of line 113, no *S. jordani* south of line 120, no *S. macdonaldi* north of line 83. Also *S. paucispinis* was not identified in the 1966 samples.

The high correlations among the first three months indicate that the sampling program provided representative estimates of larval abundance, and that short-term random changes in larval abundance do not mask annual changes during the major spawning season. Years of low abundance estimates probably indicate low spawning effort and/or high early larval mortality, whereas years of high abundance estimates indicate

TABLE 2
Estimated Rockfish Larvae (Billions) for 14 Years

	Year							
Month	1950	1951	1952	1953	1954	1955	1956	1957
Jan.	14,622	12,109	9,707	17,284	26,355	29,950	24,018	36,519
Feb.	16,118	18,715	35,049	47,529	55,980	50,871	63,875	72,650
Mar.	12,999	15,931	23,730	19,506	22,583	15,951	37,967	31,048
Apr.	16,716	25,438	14,820	8,401	16,943	16,578	9,886	30,031
May	4,593	11,414	7,575	4,496	9,447	5,810	5,763	13,457
June	4,445	9,367	9,285	4,576	7,453	5,404	4,264	8,232
July	2,969	2,580	4,652	3,467	4,858	10,993	4,295	4,591
Aug.	3,149	3,418	1,600	2,768	2,791	2,698	5,683	490
Sept.	1,433	904	1,119	2,141	1,316	987	0	701
Oct.	1,093	781	2,086	6,098	1,536	1,709	2,121	1,185
Nov.	1,109	2,462	1,801	1,486	2,110	5,192	1,376	2,083
Dec.	2,310	1,853	3,248	5,115	3,708	2,766	8,929	8,954
Totals	81,556	104,972	114,672	122,867	155,080	148,909	168,177	209,941

	Year							
Month	1958	1959	1966	1969	1972	1975	Mean	Percent
Jan.	17,424	5,777	24,736	38,560	48,378	28,617	23,861	17.68
Feb.	21,297	8,863	27,401	77,687	30,567	46,245	40,918	30.32
Mar.	15,370	4,572	23,878	40,409	30,382	28,165	23,035	17.07
Apr.	7,235	6,569	20,845	25,792	16,617	16,573	16,603	12.30
May	9,583	4,226	8,812	9,156	12,110	5,129	7,969	5.90
June	4,161	2,274	8,003	7,578	5,484	5,469	6,143	4.55
July	3,765	2,205	6,075	6,363	4,886	3,252	4,639	3.44
Aug.	113	623	1,438	3,102	2,681	2,675	2,374	1.76
Sept.	477	554	2,196	2,809	1,966	1,961	1,326	0.98
Oct.	1,300	420	1,989	1,693	2,208	1,805	1,859	1.38
Nov.	376	542	474	3,755	2,620	3,241	2,045	1.51
Dec.	1,320	1,242	3,420	2,074	4,878	8,939	4,197	3.11
Totals	82,421	37,867	129,267	218,978	162,777	152,071	134,969	100.00

Estimates are for the area represented by CalCOFI lines 60 through 137 at the time the samples were taken.

TABLE 3
Rockfish Larvae 14-Year Annual Averages

CalCOFI line	Number (billions)	Percent
60	16,044	11.841
63	15,779	11.646
67	12,685	9.362
70	5,329	3.933
73	4,201	3.101
77	6,159	4.546
Total (60-77)	60,197	44.429
80	7,476	5.518
83	12,896	9.518
87	16,326	12.049
90	9,791	7.226
93	5,094	3.760
Total (80-93)	51,583	38.071
97	3,275	2.417
100	2,973	2.194
103	1,775	1.310
107	1,419	1.048
Total (97-107)	9,442	6.969
110	1,448	1.069
113	2,014	1.486
117	3,944	2.911
120	2,182	1.610
Total (110-120)	9,588	7.076
123	1,336	0.986
127	881	0.650
130	579	0.428
133	824	0.608
137	539	0.398
Total (123-137)	4,159	3.070
140	128	0.094
143	64	0.047
147	237	0.175
150	68	0.050
153	8	0.006
157	17	0.013
Total (140-157)	522	0.385
Total (60-157)	135,491	100.000

high spawning effort and/or low early mortality rather than random fluctuations resulting from inadequate sampling.

The 14-year average number of larvae by CalCOFI line (Table 3) shows high abundance levels in the San Francisco-Monterey area (lines 60-67). These lines account for 33% of the larvae found in the main survey area (30 lines, 60-157). Sparse data for the six lines north of line 60 (lines 40-57) indicate a population equal to about 75% of the population in the area represented by the six lines 60-77, with about a third of these larvae found on line 57. Along the exposed coast south of Monterey (line 70) the larval abundance decreases to Point Conception (line 80). In the Channel Islands area (lines 83-90) larval abundance again increases. These three lines account for 29% of the larvae found in the main survey area. The number of larvae continues to decrease southward to line 157 with one smaller increase in the area around and north of Punta Eugenia and Cedros Island (lines 113-120).

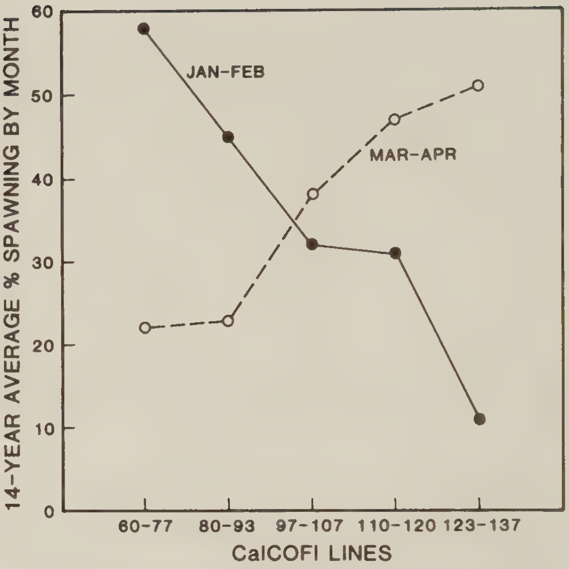

Figure 2. Percent of total year's rockfish spawning occurring in January/February and March/April for five areas as measured by larvae (14-year average).

The spawning season appears to be later farther south (Figure 2). April is the peak spawning month off Mexico (lines 97-137). This area accounts for only 17½% of the total average yearly production of rockfish larvae, in contrast to 82½% for U.S. waters (lines 60-93), which tends to mask this seasonal phenomenon (Table 3). The increase in late spawning in the more southern areas is probably due to increased proportions of late-spawning species of rockfishes like the Mexican rockfish and the subgenus *Sebastomus* (Chen 1971), which become relatively more abundant in the rockfishes' southern range.

Estimates of the numbers of all rockfishes, *S. jordani*, and *S. macdonaldi* were calculated by month and line for 1956, 1966, 1972, and 1975, and of *S. paucispinis* and *S. levis* for 1956, 1969, 1972, and 1975[1]. A summary of the estimated larval abundance by year and month (Table 4) shows that the seasonal distribution of all rockfish larvae for the 5 selected

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[1] Tables to be issued as an administrative report of the Southwest Fisheries Center.

TABLE 4
Estimated Larvae (Billions) from CalCOFI Lines 60-137 (60-157 for *Sebastes macdonaldi*) for All Rockfish, and Four Species of Rockfish

Month	Year						
All RF	1956	1966	1969	1972	1975	Mean	Percent
Jan.	24,018	24,736	38,560	48,378	28,617	32,862	19.766
Feb.	63,875	27,401	77,687	30,567	46,245	49,155	29.566
Mar.	37,967	23,878	40,409	30,382	28,165	32,160	19.344
Apr.	9,886	20,845	25,792	16,617	16,573	17,943	10.792
May	5,763	8,812	9,156	12,110	5,129	8,194	4.929
June	4,264	8,003	7,578	5,484	5,469	6,160	3.705
July	4,295	6,075	6,363	4,886	3,252	4,974	2.992
Aug.	5,683	1,438	3,102	2,681	2,675	3,116	1.874
Sept.	0	2,196	2,809	1,966	1,961	1,786	1.075
Oct.	2,121	1,989	1,693	2,208	1,805	1,963	1.181
Nov.	1,376	474	3,755	2,620	3,241	2,298	1.379
Dec.	8,929	3,420	2,074	4,878	8,939	5,648	3.397
Totals	168,177	129,267	218,978	162,777	152,071	166,254	100.000
S. paucispinis							
Jan.	548		2,651	3,966	2,050	2,304	40.131
Feb.	351		2,934	1,615	1,693	1,648	28.713
Mar.	514		1,374	1,388	952	1,057	18.413
Apr.	65		462	333	235	274	4.769
May	17		170	304	82	143	2.495
June	17		20	17	24	20	0.340
July	0		0	0	0	0	0.000
Aug.	0		0	0	0	0	0.000
Sept.	0		0	0	0	0	0.000
Oct.	0		0	13	6	5	0.083
Nov.	0		12	12	19	11	0.187
Dec.	133		168	341	476	280	4.869
Totals	1,645		7,791	7,989	5,537	5,742	100.000
S. jordani							
Jan.	1,611	2,761	1,611	3,551	2,160	2,339	13.564
Feb.	14,300	8,118	20,932	2,426	10,590	11,273	65.378
Mar.	2,962	2,017	4,186	2,541	2,419	2,825	16.383
Apr.	492	667	1,183	364	666	674	3.911
May	23	0	113	310	46	98	0.571
June	0	0	9	1	3	3	0.015
July	0	0	4	0	0	1	0.005
Aug.	0	0	23	11	21	11	0.064
Sept.	0	0	0	0	0	0	0.000
Oct.	0	0	0	0	0	0	0.000
Nov.	0	0	17	11	66	19	0.109
Dec.	0	0	0	0	0	0	0.000
Totals	19,388	13,563	28,078	9,215	15,971	17,243	100.000
S. levis							
Jan.	40		56	214	574	221	45.473
Feb.	0		170	53	164	97	19.908
Mar.	0		93	118	144	89	18.261
Apr.	8		119	7	139	68	14.043
May	0		15	7	0	6	1.132
June	0		0	0	0	0	0.000
July	0		23	0	0	6	1.183
Aug.	0		0	0	0	0	0.000
Sept.	0	0		0	0	0	0.000
Oct.	0	0		0	0	0	0.000
Nov.	0		0	0	0	0	0.000
Dec.	0	0		0	0	0	0.000
Totals	48		476	399	1,021	487	100.000

(Table 4 continued on next page)

TABLE 4 (continued)

Month	Year						
	1956	1966	1969	1972	1975	Mean	Percent
S. macdonaldi							
Jan.	268	36	86	35	167	118	10.432
Feb.	279	437	637	125	153	326	28.740
Mar.	67	473	298	750	7	319	28.106
Apr.	17	979	172	459	162	358	31.524
May	17	0	6	7	2	6	0.564
June	0	0	0	0	0	0	0.000
July	0	0	0	0	0	0	0.000
Aug.	0	0	0	0	0	0	0.000
Sept.	0	0	0	0	0	0	0.000
Oct.	0	0	0	0	0	0	0.000
Nov.	0	10	0	3	0	3	0.299
Dec.	0	0	18	5	0	5	0.405
Totals	648	1,935	1,217	1,384	491	1,135	100.000

years is not much different from the 14-year average of which it is a part (Table 2). However, the 5 years were among the years of higher abundance estimates. The mean abundance index was 166×10^{12} compared to 135×10^{12} for the 14-year average.

For the 5 years in which individual species were enumerated, 30% of all rockfish larvae were taken in February, 20% in January, 19% in March, and 11% in April (Figure 3). *S. jordani*, which accounted for 10.4% of all rockfish larvae, was most abundant in February in 4 of 5 years; an average of 65% of the larvae was taken in this month. January, February, and March accounted for 95% of the larvae of this species. The larvae of *S. paucispinis* were most abundant in January, when 40% of the estimated annual number was found. In January, February, and March—the months of heaviest spawning—87% of the annual larval population of this species was present. *S. paucispinis* was about one-third as abundant as *S. jordani*. *S. levis* also appears to be an earlier-spawning species, with 45% of the spawning taking place in January. In January, February, and March 84% of the larvae were taken. *S. levis* larvae were only 1/35 as abundant as *S. jordani* larvae. *S. macdonaldi* appeared to be a later-spawning species, with 32% of the spawning occurring in April. About 89% of the total larvae were taken in February, March, and April. *S. macdonaldi* larvae were about 1/15 as abundant as *S. jordani* larvae.

The distribution of all rockfish larvae by line for the 5 years (Table 5; Figure 4) is not much different from the distribution for the 14 years (Table 3).

The distribution of *S. jordani* larvae by line and year (Table 6) indicates concentrations in the San Francisco-Monterey area (lines 60-67), where 53% of the 5-year mean of the number of larvae occurred, and in the Channel Islands area (lines 83-90), where 35% of the larvae were found. No larvae were taken south of line 120 (Cedros Island). No data are available for the area north of line 60.

S. paucispinis larvae appear to follow all rockfish larvae in distribution by line within their range (Table 7). They were most abundant in the Channel Islands

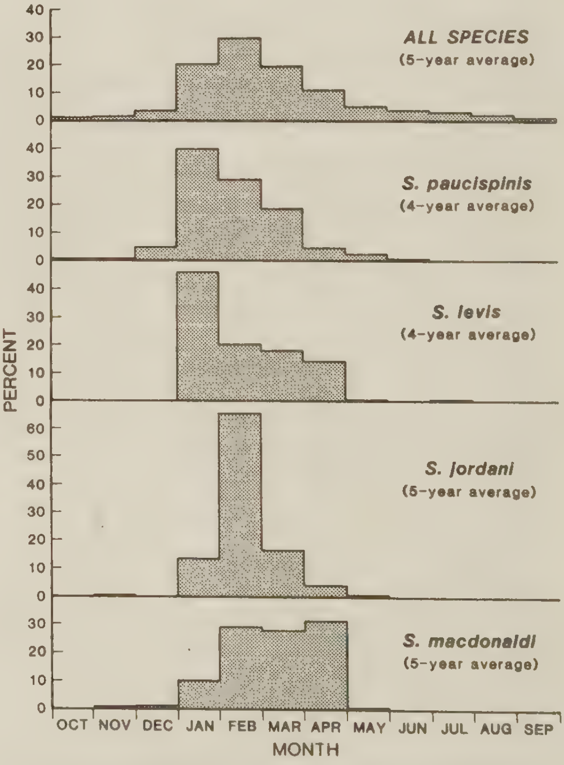

Figure 3. Percent spawning by month as indicated by larval rockfish taken in net tows.

TABLE 5
Percent Distribution of Rockfish Larvae by CalCOFI Line

Line	Year 1956	1966	1969	1972	1975	Average
60	13.240	12.455	14.933	11.926	10.560	12.816
63	11.490	12.303	14.494	6.569	11.926	11.524
67	9.944	12.232	10.361	6.752	8.439	9.509
70	4.065	5.449	4.660	4.840	4.496	4.668
73	2.879	3.170	3.098	2,869	4.421	3.262
77	4.369	5.615	4.543	8.468	3.481	5.249
60-77	45.987	51.224	52.089	41.424	43.323	47.028
80	3.213	4.578	4.710	10.494	4.644	5.507
83	7.070	10.832	11.112	14.634	13.469	11.372
87	11.556	11.068	11.713	10.566	15.135	11.983
90	8.945	5.354	8.845	9.741	7.834	8.312
93	1.978	3.027	2.502	3.441	2.976	2.748
80-93	32.762	34.859	38.882	48.876	44.058	39.922
97	0.824	1.901	0.966	2.118	1.603	1.425
100	2.520	2.849	1.226	1.352	1.631	1.839
103	1.738	0.673	0.649	0.750	1.365	1.024
107	1.993	0.952	0.832	0.419	0.775	0.994
97-107	7.075	6.375	3.673	4.639	5.374	5.282
110	1.486	1.176	0.992	0.515	0.975	1.024
113	1.148	1.036	0.778	0.549	0.874	0.866
117	4.479	2.321	1.283	1.240	2.123	2.236
120	3.689	0.860	0.844	0.800	1.500	1.533
110-120	10.802	5.393	3.897	3.104	5.472	5.659
123	1.013	1.137	0.636	0.937	0.545	0.833
127	0.930	0.383	0.255	0.413	0.537	0.494
130	0.228	0.112	0.093	0.077	0.179	0.136
133	0.568	0.230	0.226	0.270	0.187	0.297
137	0.501	0.142	0.156	0.143	0.189	0.227
123-137	3.240	2.004	1.366	1.840	1.637	1.987
140	0.065	0.073	0.045	0.055	0.069	0.060
143	0.041	0.041	0.028	0.033	0.045	0.036
147	0.000	0.000	0.000	0.000	0.000	0.000
150	0.009	0.009	0.006	0.010	0.006	0.008
153	0.008	0.041	0.006	0.007	0.008	0.008
157	0.011	0.011	0.008	0.012	0.008	0.010
140-157	0.134	0.145	0.093	0.117	0.136	0.122
60-157	100.000	100.000	100.000	100.000	100.000	100.000

area off southern California, and north to Point Conception. Nineteen percent of the larvae occurred in the area represented by line 83, and 53% in the area represented by lines 80-90. The peak on lines 60-67 is less marked than for all rockfish, and there are no data for the area to the north.

The distribution of *S. levis* (Table 8) appears to be restricted primarily to southern California. Miller and Lea (1972) give the range of this species as from Mendocino County (line 50) to Ranger Bank (line 117). Most larvae—86%—were taken on lines 83-90. Only 7% occurred in the area represented by the six lines north of Point Conception.

S. macdonaldi (Table 9) has the most southerly distribution of the four species. No larvae were taken from Point Conception (line 80) north. Ninety-seven percent of the larvae were spread over the area represented by the 10 lines 110-140, with 37% occurring along line 117. A second apparent peak was found south of Point Eugenia along line 123. The population decreased to line 143 (Magdalena Bay area), and no larvae were taken to the south.

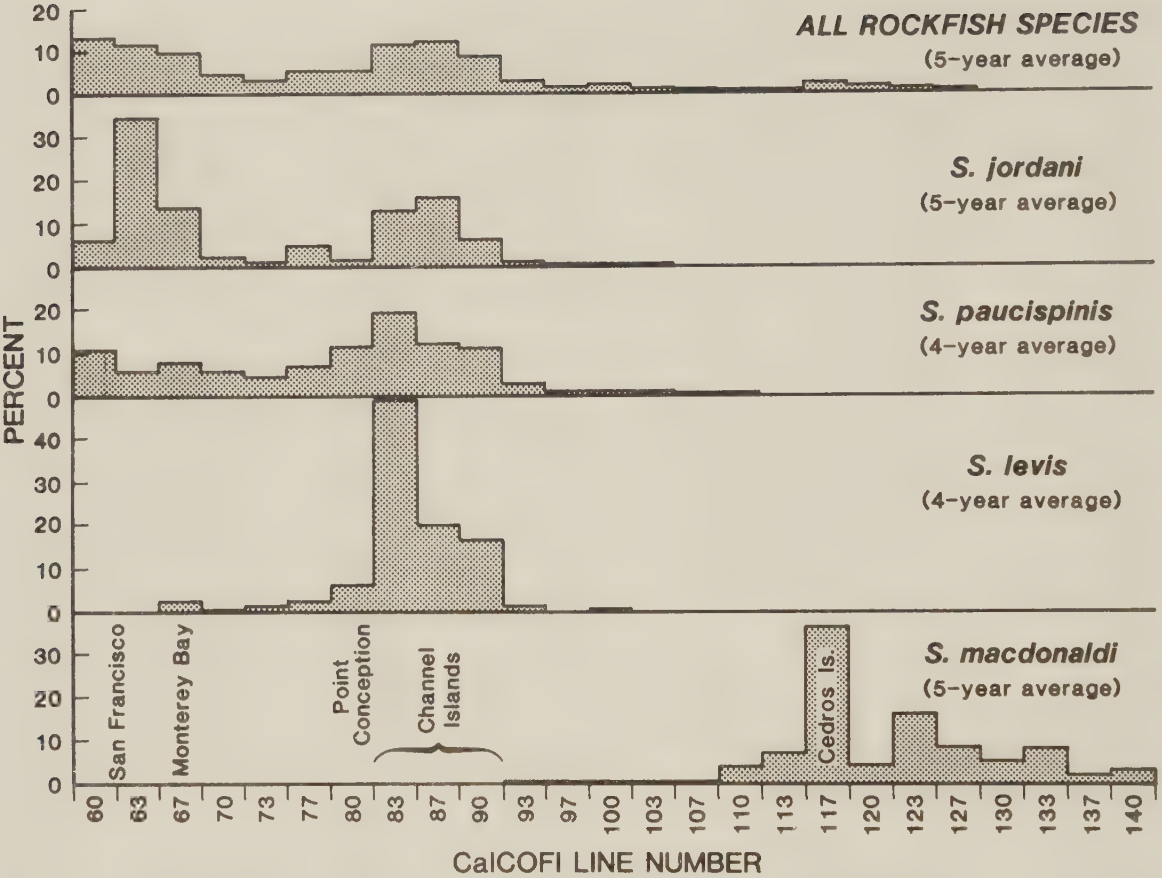

Figure 4. Larval rockfish percent distribution by CalCOFI line.

S. jordani, the most abundant of the four identified species, accounted for 10.4% of all rockfish larvae taken on lines 60-137 (Table 10). It was most abundant between San Francisco and Monterey (lines 63 and 67), where *S. jordani* was 23.4% of all rockfish larvae, and in the Channel Islands (lines 83 and 87), where it was 12.9% of all larvae. *S. paucispinis* accounted for 3.27% of all rockfish larvae. Its distribution was disproportionately high between the abundance peaks of all rockfish larvae. In this area (lines 70-80) it accounted for 5.0% of all rockfish larvae. *S. levis* was the least abundant of the four species, constituting only 0.28% of all rockfishes. It was most abundant in the Channel Islands area, where it accounted for 0.73% of the larvae on the three lines 83-90. *S. macdonaldi* larvae amounted to 0.68% of the total rockfish larvae. They were most abundant on line 117, where they equalled 11.14% of all rockfish larvae. However, smaller numbers of *S. macdonaldi* to the south of this area constituted a larger portion of the population (up to 27.8% on line 130) as numbers of other species decreased rapidly.

Length compositions (Tables 11-14) for *S. jordani* and *S. paucispinis* show an apparent increase in the percent of larger larvae as the season progresses; this is not apparent for the two less-abundant species. However, most of the larvae for all four species are smaller, more recently hatched larvae.

Moser et al. (1977) give the size of newly hatched *S. paucispinis* and *S. macdonaldi* as 4.5 mm, *S. levis* as 5.0 mm, and *S. jordani* as 5.4 mm. About 87% of *S. jordani*, 78% of *S. paucispinis*, 83% of *S. macdonaldi*, and 70% of *S. levis* were within 1 mm of the size of newly hatched larvae (Figure 5). This indicates that, unless rockfish larvae have exceptionally slow growth, a large portion of captured larvae were spawned during the month of capture. The decrease in numbers of longer larvae indicates a very high mortality combined

TABLE 6
Percent Distribution of *Sebastes jordani* Larvae by CalCOFI Line

Line	Year 1956	1966	1969	1972	1975	Average
60	5.875	5.190	5.805	6.989	6.906	6.055
63	35.976	30.229	38.977	22.398	36.535	34.701
67	12.554	16.560	12.925	6.424	12.949	12.723
70	1.547	2.625	2.148	3.039	1.703	2.100
73	0.928	0.509	1.079	0.846	2.285	1.154
77	4.513	5.766	4.861	4.775	3.995	4.756
60-77	61.393	60.879	65.795	44.471	64.373	61.489
80	0.423	0.819	2.799	1.357	1.903	1.633
83	12.111	15.483	8.594	26.088	12.316	13.028
87	18.207	17.105	15.468	11.915	15.879	16.038
90	5.555	4.394	6.336	14.704	3.970	6.311
93	0.753	0.605	0.641	1.020	0.488	0.673
80-93	37.049	38.406	33.838	55.084	34.556	37.683
97	0.031	0.288	0.103	0.141	0.507	0.195
100	0.676	0.383	0.185	0.108	0.338	0.347
103	0.660	0.015	0.018	0.000	0.163	0.187
107	0.000	0.000	0.025	0.011	0.013	0.011
97-107	1.367	0.686	0.331	0.260	1.021	0.740
110	0.191	0.000	0.000	0.000	0.050	0.052
113	0.000	0.000	0.000	0.000	0.000	0.000
117	0.000	0.029	0.032	0.185	0.000	0.035
120	0.000	0.000	0.004	0.000	0.000	0.001
110-120	0.191	0.029	0.036	0.185	0.050	0.088
123-157	0.000	0.000	0.000	0.000	0.000	0.000
60-157	100.000	100.000	100.000	100.000	100.000	100.000

with increasing ability to dodge the net as the larvae develop and grow. The decrease also may be affected by differences in growth rates among the species.

Exponential equations fitted to the data by transforming catches to logarithms and then using standard least squares regression techniques indicate a 61%

TABLE 7
Percent Distribution of *Sebastes paucispinis* Larvae by CalCOFI Line

Line	Year 1956	1969	1972	1975	Average
60	12.462	9.703	15.296	5.261	10.774
63	6.079	8.895	1.940	6.003	5.575
67	7.355	12.091	3.980	5.985	7.456
70	5.836	4.698	5.232	7.304	5.618
73	4.924	4.646	2.616	7.431	4.629
77	6.809	5.776	8.512	5.496	6.733
60-77	43.465	45.809	37.576	37.480	40.785
80	8.632	9.986	12.467	13.560	11.611
83	12.644	19.073	21.430	17.158	18.966
87	14.347	11.693	9.751	14.211	11.811
90	14.225	9.126	10.802	12.746	10.944
93	1.824	2.978	3.655	1.356	2.739
80-93	51.672	52.856	58.105	59.031	56.071
97	1.155	0.500	2.028	0.958	1.189
100	2.371	0.488	1.027	0.651	0.849
103	0.425	0.257	0.851	1.537	0.784
107	0.000	0.051	0.225	0.036	0.104
97-107	3.951	1.296	4.131	3.182	2.926
110	0.182	0.039	0.188	0.307	0.166
113	0.730	0.000	0.000	0.000	0.052
117	0.000	0.000	0.000	0.000	0.000
120	0.000	0.000	0.000	0.000	0.000
110-120	0.912	0.039	0.188	0.307	0.218
123-157	0.000	0.000	0.000	0.000	0.000
60-157	100.000	100.000	100.000	100.000	100.000

TABLE 8
Percent Distribution of *Sebastes levis* Larvae by CalCOFI Line

	Year				
Line	1956	1969	1972	1975	Average
60	0.000	0.000	0.000	0.000	0.000
63	0.000	0.000	0.000	0.000	0.000
67	2.083	6.513	0.000	1.371	2.377
70	2.083	1.681	0.000	0.000	0.465
73	2.083	0.630	0.000	2.057	1.292
77	2.084	5.252	6.154	0.000	2.584
60-77	8.333	14.076	6.154	3.428	6.718
80	0.000	8.824	7.436	4.799	6.202
83	0.000	22.689	40.769	66.993	49.147
87	39.583	27.731	31.282	11.460	20.155
90	52.084	21.639	14.359	13.320	16.538
93	0.000	3.151	0.000	0.000	0.775
80-93	91.667	84.034	93.846	96.572	92.817
97	0.000	0.000	0.000	0.000	0.000
100	0.000	1.260	0.000	0.000	0.310
103	0.000	0.000	0.000	0.000	0.000
107	0.000	0.000	0.000	0.000	0.000
97-107	0.000	1.260	0.000	0.000	0.310
110	0.000	0.000	0.000	0.000	0.000
113	0.000	0.000	0.000	0.000	0.000
117	0.000	0.630	0.000	0.000	0.155
120	0.000	0.000	0.000	0.000	0.000
110-120	0.000	0.630	0.000	0.000	0.155
123-152	0.000	0.000	0.000	0.000	0.000
60-157	100.000	100.000	100.000	100.000	100.000

TABLE 9
Percent Distribution of *Sebastes macdonaldi* Larvae by CalCOFI Line

	Year					
Line	1956	1966	1969	1972	1975	Average
60-77	0.000	0.000	0.000	0.000	0.000	0.000
80	0.000	0.000	0.000	0.000	0.000	0.000
83	0.000	0.000	1.479	0.361	0.000	0.405
87	0.000	0.000	0.000	0.000	0.000	0.000
90	0.000	0.000	0.000	0.000	0.000	0.000
93	0.000	0.413	0.000	0.000	0.000	0.141
80-93	0.000	0.413	1.479	0.361	0.000	0.5464
97	0.000	0.310	0.000	0.145	0.204	0.159
100	0.000	0.052	0.740	0.361	0.204	0.282
103	2.932	0.000	0.000	0.000	0.407	0.370
107	0.000	0.000	2.136	0.289	0.611	0.581
97-107	2.932	0.362	2.876	0.795	1.426	1.392
110	9.722	2.791	4.601	1.300	7.943	4.053
113	2.469	5.530	7.560	6.142	24.236	7.384
117	12.191	50.749	25.301	40.607	27.902	36.546
120	6.019	2.635	5.423	5.997	1.222	4.317
110-120	30.401	61.705	43.385	54.046	61.303	52.300
123	35.494	11.576	19.392	13.512	10.998	16.405
127	4.938	7.804	15.366	4.552	12.831	8.740
130	17.901	4.238	2.711	4.046	5.499	5.533
133	0.000	7.338	7.231	16.257	2.037	8.194
137	2.624	2.016	3.205	2.023	1.629	2.309
123-137	60.957	32.972	47.905	40.390	32.994	41.181
140	4.321	3.876	3.287	3.396	3.055	3.612
143	1.389	0.672	1.068	1.012	1.222	0.969
147	0.000	0.000	0.000	0.000	0.000	0.000
150	0.000	0.000	0.000	0.000	0.000	0.000
153	0.000	0.000	0.000	0.000	0.000	0.000
157	0.000	0.000	0.000	0.000	0.000	0.000
140-157	5.710	4.548	4.355	4.408	4.277	4.581
60-157	100.000	100.000	100.000	100.000	100.000	100.000

TABLE 10
Estimated Mean Numbers of Rockfish (for 1956, 1966, 1969, 1972, 1975) and Percent Each Species Is of All Rockfish

Line	5-year average					4-year average				
	All rockfish	*S. jordani*		*S. macdonaldi*		All rockfish	*S. paucispinis*		*S. levis*	
	No.	No.	%	No.	%	No.	No.	%	No.	%
60	21,333	1,004	4.89	0	0.00	22,636	619	2.73	0	0.00
63	19,182	5,984	31.19	0	0.00	19,996	320	1.60	0	0.00
67	15,829	2,194	13.86	0	0.00	15,827	428	2.70	12	0.07
70	7,770	362	4.66	0	0.00	7,948	322	4.06	2	0.03
73	5,430	199	3.67	0	0.00	5,762	266	4.61	6	0.11
77	8,737	820	9.39	0	0.00	9,104	386	4.25	13	0.14
Total	78,281	10,603	13.54	0	0.00	81,273	2,341	2.88	33	0.04
80	9,167	282	3.07	0	0.00	9,977	667	6.68	30	0.30
83	18,929	2,247	11.87	5	0.02	20,155	1,089	5.40	238	1.18
87	19,945	2,765	13.87	0	0.00	21,350	678	3.18	98	0.46
90	13,836	1,088	7.87	0	0.00	15,563	628	3.39	80	0.51
93	4,575	116	2.54	2	0.04	4,739	157	3.32	4	0.08
Total	66,452	6,498	9.78	7	0.01	71,784	3,219	4.48	449	0.63
97	2,372	34	1.42	2	0.08	2,349	68	2.91	0	0.00
100	3,061	60	1.95	3	0.11	2,905	49	1.68	2	0.05
103	1,704	32	1.89	4	0.25	1,912	45	2.35	0	0.00
107	1,655	2	0.12	7	0.40	1,761	6	0.34	0	0.00
Total	8,792	128	1.45	16	0.18	8,927	168	1.88	2	0.02
110	1,704	9	0.53	46	2.70	1,750	10	0.54	0	0.00
113	1,441	0	0.00	84	5.82	1,466	3	0.21	0	0.00
117	3,723	6	0.16	415	11.14	3,902	0	0.00	3	0.08
120	2,553	+	0.01	49	1.92	2,913	0	0.00	0	0.00
Total	9,421	15	0.16	594	6.30	10,031	13	0.13	3	0.03
123	1,386	0	0.00	186	13.44	1,365	0	0.00	0	0.00
127	822	0	0.00	99	12.06	904	0	0.00	0	0.00
130	226	0	0.00	63	27.79	246	0	0.00	0	0.00
133	495	0	0.00	93	18.80	544	0	0.00	0	0.00
137	378	0	0.00	26	6.93	427	0	0.00	0	0.00
Total	3,307	0	0.00	467	14.13	3,486	0	0.00	0	0.00
140-157	203	0	0.00	52	25.59	207	0	0.00	0	0.00
All lines	166,457	17,243	10.36	1,135	0.68	175,708	5,740	3.27	486	0.28

decrease in numbers with each mm of length growth for *S. jordani*. The decrease is 58% for *S. macdonaldi*, 54% for *S. levis*, and 43% for *S. paucispinis*. *S. jordani* is a small species and may have slower-growing larvae. *S. paucispinis* grows more rapidly than other rockfish later in life and may also have faster-growing larvae. The differences in decrease in numbers of larvae may reflect these growth differences rather than temporal mortality.

The larval abundance estimates yield interesting data on relative numbers of larvae by year, month, and area of the four species in relation to all larvae and to each other. But we need additional data in order to estimate the total numbers of larvae produced each year and, from that, the biomass of the spawning population. The two most important missing elements are the growth of larvae with time and temperature, and larval mortality. With these data we could interpolate for between-cruise estimates and obtain a rough estimate of the total annual production for each identified species. In order to convert larval data to adult biomass we need data on species size at maturity, ratio of adult females to males, number of larvae produced per unit weight of females per spawning, and number of spawnings per year. According to Phillips (1964), a few *S. jordani* mature at 6″ total length (152 mm, 31 g), age 2; 50% at 6½″ (165 mm, 30 g), age 3. They attain a maximum size of 12″ (306 mm, 275 g) and age of 10 years. A few *S. paucispinis* spawn at 14″ TL (356 mm, 456 g), age 3; 50% mature at 16¼″ (413 mm, 723 g),

TABLE 11
Number and Percent of *Sebastes paucispinis* by Size and Month*

Length	Number (billions)										
(mm)	Jan.	Feb.	Mar.	Apr.	May	June	Oct.	Nov.	Dec.	Total	Percent
2.0	10.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.7	0.19
2.5	40.2	20.5	0.0	0.0	0.0	0.0	0.0	0.0	13.4	74.1	1.30
3.0	96.3	5.8	5.4	14.6	4.3	0.0	0.0	0.0	49.2	175.6	3.08
3.5	291.7	38.1	21.9	19.4	8.6	0.0	0.0	0.0	35.8	415.5	7.28
4.0	696.0	278.3	137.0	43.7	4.3	5.9	3.1	0.0	53.7	1,222.0	21.40
4.5	422.9	389.8	230.1	48.6	8.6	0.0	3.1	4.3	49.2	1,156.6	20.26
5.0	275.7	383.8	246.6	29.1	8.6	5.9	0.0	4.3	17.9	971.9	17.02
5.5	165.9	140.7	71.3	19.4	0.0	0.0	0.0	0.0	8.9	406.2	7.11
6.0	101.7	149.4	60.3	9.7	17.2	0.0	0.0	0.0	8.9	347.2	6.08
6.5	45.5	43.9	60.3	4.9	12.9	0.0	0.0	0.0	0.0	167.5	2.93
7.0	56.2	88.0	43.9	9.7	4.3	0.0	0.0	0.0	0.0	202.1	3.54
7.5	34.8	26.4	21.9	4.9	8.6	0.0	0.0	0.0	0.0	96.6	1.69
8.0	16.0	79.1	27.4	4.9	0.0	0.0	0.0	0.0	0.0	127.4	2.23
8.5	21.4	35.2	21.9	14.6	8.6	0.0	0.0	0.0	4.5	106.2	1.86
9.0	13.5	29.4	16.4	4.9	4.3	0.0	0.0	0.0	4.5	73.0	1.28
9.5	5.3	8.7	5.4	0.0	0.0	0.0	0.0	0.0	0.0	19.4	0.34
10.0	16.0	11.7	5.4	0.0	4.3	0.0	0.0	0.0	4.5	41.9	0.73
10.5	0.0	3.0	5.4	0.0	0.0	0.0	0.0	0.0	0.0	8.4	0.15
11.0	5.3	3.0	11.0	0.0	4.3	0.0	0.0	0.0	0.0	23.6	0.41
11.5	2.8	5.8	5.4	0.0	4.3	0.0	0.0	0.0	0.0	18.3	0.32
12.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.05
12.5	0.0	0.0	0.0	4.9	4.3	0.0	0.0	0.0	0.0	9.2	0.16
13.0	0.0	0.0	5.4	0.0	0.0	0.0	0.0	0.0	0.0	5.4	0.10
13.5	0.0	3.0	0.0	9.7	0.0	0.0	0.0	0.0	0.0	12.7	0.22
14.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.05
14.5	0.0	0.0	5.4	0.0	0.0	0.0	0.0	0.0	0.0	5.4	0.10
—											
16.0	0.0	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	4.3	0.07
—											
18.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.05
Total	2,320.7	1,749.6	1,007.8	243.0	111.8	11.8	6.2	8.6	250.5	5,710.0	100.00
Percent	40.645	30.637	17.654	4.253	1.958	0.206	0.108	0.152	4/387		100.00

*Average data for all years.

TABLE 12
Number and Percent of *Sebastes levis* by Size and Month*

Length	Number (billions)								
(mm)	Jan.	Feb.	Mar.	Apr.	May	July	Dec.	Total	Percent
4.0	45.7	0.0	5.5	0.0	0.0	0.0	4.0	55.2	11.19
4.5	35.5	3.2	13.8	21.8	0.6	0.0	0.0	75.0	15.21
5.0	35.5	9.6	30.4	10.9	0.0	0.0	3.9	90.5	18.35
5.5	20.3	6.4	16.6	5.5	0.0	0.0	0.0	48.8	9.90
6.0	25.4	16.1	13.8	16.4	0.0	5.9	0.0	77.6	15.73
6.5	20.3	28.9	8.3	0.0	0.0	0.0	3.9	61.5	12.46
7.0	10.2	6.4	2.8	0.0	0.6	0.0	0.0	19.9	4.04
7.5	20.3	3.2	5.5	10.9	0.0	0.0	0.0	40.0	8.11
8.0	15.2	3.2	0.0	0.0	0.6	0.0	0.0	19.0	3.86
8.5	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.6	0.12
—									
10.0	5.1	0.0	0.0	0.0	0.0	0.0	0.0	5.1	1.03
Total	233.5	77.1	96.8	65.5	2.3	5.9	11.8	493.1	100.00
Percent	47.36	15.64	19.64	13.29	0.47	1.20	2.40		100.00

*Average data for all years.

TABLE 13
Number and Percent of *Sebastes macdonaldi* by Size and Month*

Length (mm)	Number (billions)								
	Jan.	Feb.	Mar.	Apr.	May	Nov.	Dec.	Total	Percent
3.5	0.0	0.0	0.0	8.6	0.0	0.0	0.0	8.6	0.74
4.0	22.5	22.1	68.6	86.4	1.1	0.0	0.0	200.7	17.19
4.5	28.9	119.3	103.0	83.5	2.7	2.4	0.0	339.8	29.11
5.0	33.7	68.5	76.6	103.6	0.2	2.4	0.0	285.0	24.42
5.5	20.9	68.5	10.6	31.7	0.2	0.0	0.0	131.9	11.29
6.0	4.8	37.6	7.9	40.3	0.4	0.0	0.0	91.0	7.79
6.5	0.0	8.8	13.2	2.9	0.0	0.0	0.0	24.9	2.14
7.0	6.4	6.6	5.3	2.9	0.0	0.0	0.0	21.2	1.82
7.5	0.0	13.3	0.0	2.9	0.0	0.0	0.0	16.2	1.38
8.0	1.6	6.6	0.0	5.7	0.5	0.0	0.0	14.4	1.24
8.5	0.0	2.2	0.0	5.7	0.0	0.0	0.0	7.9	0.68
9.0	0.0	2.2	0.0	0.0	0.0	0.0	0.0	2.2	0.19
9.5	0.0	4.4	0.0	5.7	0.0	0.0	4.5	14.6	1.26
10.0	0.0	2.2	0.0	0.0	0.5	0.0	0.0	2.7	0.23
10.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00
11.0	0.0	0.0	0.0	2.9	0.0	0.0	0.0	2.9	0.25
—									
12.5	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.01
—									
14.5	0.0	0.0	0.0	2.9	0.0	0.0	0.0	2.9	0.25
15.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.01
Total	118.8	362.3	285.2	385.7	6.0	4.8	4.5	1,167.3	100.00
Percent	10.18	31.03	24.44	33.04	0.50	0.42	0.39		100.00

TABLE 14
Number and Percent of *Sebastes jordani* by Size and Month*

Length (mm)	Number (billions)										
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Nov.	Total	Percent
4.0	28.8	0.0	3.6	0.0	4.3	0.0	0.0	0.0	7.3	44.0	0.25
4.5	558.9	210.7	114.7	13.0	0.0	0.0	0.0	0.0	2.5	899.8	5.18
5.0	862.6	2,935.5	696.0	123.3	12.9	0.0	0.4	11.2	7.3	4,649.2	26.77
5.5	592.7	3,080.6	721.3	100.6	21.4	0.0	0.4	11.2	2.4	4,530.6	26.09
6.0	222.5	2,177.7	351.6	220.7	12.9	0.0	0.0	0.0	2.4	2,987.8	17.20
6.5	73.0	1,846.0	157.8	58.4	8.6	0.0	0.0	0.0	0.0	2,143.8	12.35
7.0	45.9	738.2	136.4	42.2	0.0	0.0	0.0	0.0	0.0	962.7	5.54
7.5	20.3	322.5	86.0	42.2	0.0	0.0	0.0	0.0	0.0	471.0	2.71
8.0	8.5	115.2	75.4	32.5	8.6	0.0	0.0	0.0	0.0	240.2	1.38
8.5	5.1	49.5	43.1	22.7	0.0	0.0	0.0	0.0	0.0	120.4	0.69
9.0	0.0	28.8	64.6	19.5	4.3	0.0	0.0	0.0	0.0	117.2	0.67
9.5	0.0	2.9	43.1	13.0	0.0	0.0	0.0	0.0	0.0	59.0	0.34
10.0	0.0	2.9	43.1	16.2	0.0	0.0	0.0	0.0	0.0	62.2	0.36
10.5	0.0	0.0	25.1	3.3	0.0	0.0	0.0	0.0	0.0	28.4	0.16
11.0	0.0	2.9	17.8	3.3	0.0	0.0	0.0	0.0	0.0	24.0	0.14
11.5	0.0	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	4.3	0.03
12.0	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	3.6	0.02
12.5	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	3.3	0.02
13.0	0.0	2.9	0.0	3.3	0.0	0.0	0.0	0.0	0.0	6.2	0.04
13.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	3.0	0.02
—											
21.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	3.3	0.02
—											
24.5	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	3.3	0.02
Total	2,418.3	11,516.3	2,583.2	724.1	77.3	3.0	0.8	22.4	21.9	17,367.3	100.00
Percent	13.925	66.310	14.875	4.168	0.444	0.017	0.005	0.129	0.127		100.00

*Average data for all years.

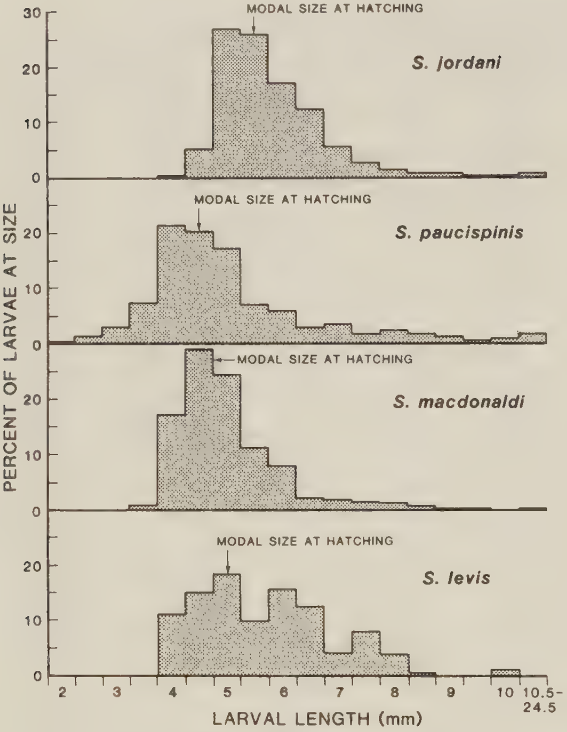

Figure 5. Percent length distribution of larval rockfish.

age 4. They live to a maximum age of 30 years and attain a maximum size of 34″ (864 mm, 7096 g).

Phillips (1964) also gives fecundity data for these two species. Both show an increase in relative as well as absolute fecundity with increasing size of fish. Based on ten specimens of *S. jordani* weighing 46 to 275 g, a 50-g fish should produce an average of 115 eggs (larvae) per gram of spawning female fish, while a 275-g fish should produce 139 eggs/g. For *S. paucispinis* (based on 24 specimens weighing 560 to 5000 g) the relative fecundity was 200 eggs/g for a 550-g fish and 434 eggs/g for a 5000-g fish.

The average fecundity for Phillips' *S. Jordani* sample was 134 eggs/g, and for his *S. paucispinis* sample 339 eggs/g. A sample of 13 *S. paucispinis* from Fortymile Bank off southern California (MacGregor 1970) had an average fecundity of 211 eggs/g. These fish were smaller than Phillips' sample from the Monterey area.

We believe that rockfish spawn twice a year (Moser 1967; MacGregor 1970). Based on the ten specimens of *S. jordani*, this would mean that 268 larvae represent one gram of spawning female (if we discount larval mortality for present purposes); 610 larvae represent one gram of spawning female *S. paucispinis* (based on the combined total of 37 fish). The average number of *S. paucispinis* larvae found in the survey area for the four years was 5.7 trillion, with about three times as many *S. jordani*, 17.2 trillion. Based on the difference in relative fecundity, and assuming equal larval mortality rates, the spawning biomass of *S. jordani* should be about seven times larger than that of *S. paucispinis*.

In estimating the population of larvae present in the survey area, I have used a very small sampled area expanded to a population estimate for a very large area. I do not know how accurate this expansion is. However, the larval data are more consistent within years and among years than for egg and larval data of other species that have been studied in the CalCOFI area. As mentioned earlier, in years when rockfish larvae are more abundant, they tend to be abundant throughout the area and spawning season; when less abundant, they are consistently less abundant throughout the area and season. This would indicate that years of low larval abundance are truly years of scarcity, and years of high larval abundance are truly years of greater spawning success, and that these changes in abundance are not the result of erratic distribution.

Although the total production of *Sebastes* larvae varies from year to year, the numbers of larvae taken on each line remain proportionally similar both for all larvae and for the more abundant identified species. Both the season and area of spawning remained remarkably stable for the four species for the 4 or 5 years of the survey and for all species for the 14 years of data. However, all species do not have good spawning years at the same time. The second best year for *S. jordani* (1956) produced the smallest number of larvae for the other three species, and the year of smallest *S. jordani* larval production (1972) was the best or second best for the other three species.

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8665

Environmental Influences on the French, Ivory Coast, Senegalese and Moroccan Tuna Catches in the Gulf of Guinea

R. Mendelssohn

Pacific Environmental Group, SWFC, NMFS, NOAA, P.O. Box 831, Monterey, Ca. 93942, U.S.A.

and Ci Roy[1]

Antenne ORSTOM, Centre Océanologique de Bretagne, B.P. 337, 29273 Brest Cédex, France

Both local and broadscale dynamic relationships were studied between catch per unit of effort (CPUE) for yellowfin and skipjack tunas in the Gulf of Guinea, and sea-surface temperatures (SST), and wind speed. The results suggested why a particular temperature during one time period will lead to high CPUE, while at another it will lead to low CPUE. Our analysis was not restricted to where fishing actually occurred.

We used a recently developed algorithm to complete missing CPUE and environmental data. Models were developed for eleven separate sub-areas of the Gulf of Guinea. Details of the method are provided in an appendix. Results from these models suggested that the environmental variables under study reflected an oceanographic process involving upwelling and concentration of nutrients a month prior to good fishing, followed by arrival of relatively warmer waters two weeks prior to good fishing.

We calculated dominant modes of variability for each parameter in time and space by six week and one year periods. The dominant mode for SST showed a space-time movement that was consistent with a recently developed theory of remote forcing in the equatorial Atlantic.

The dominant modes for CPUE for both yellowfin and skipjack showed relatively little discernible pattern. However, when dominant modes were calculated between SST and CPUE for the same periods and species of fish, the CPUE exhibited the same movement in space and time as SST, at about the same speed. This suggested the predictability of CPUE was largely due to a broadscale oceanographic process, which may have been associated with remote forcing in that region.

On a étudié les relations de la dynamique locale et à grande échelle entre la prise par unité d'effort (CPUE) de l'albacore et du listao dans le golfe de Guinée, les températures de surface (SST) et la vitesse du vent. Les résultats montrent pourquoi une température déterminée durant une période donne une CPUE élevée, alors qu'à une autre période elle entraîne une CPUE faible. Notre étude ne s'est pas limitée aux lieux de pêche actuels.

Pour obtenir les données de CPUE et de milieu manquantes, nous avons utilisé un algorithme récemment développé. Des modèles ont été établis dans le golfe de Guinée et ceci dans onze sous-zones séparées. Les détails de cette méthode indiquent que les variables de milieu sous étude reflétaient un procédé océanographique comportant un affleurement et une concentration d'aliments un mois avant une pêche fructueuse, suivi de l'arrivé d'eaux relativement plus chaudes, deux semaines avant une bonne pêche.

Nous avons calculé les principaux modes de variabilité de chaque paramètre dans le temps et dans l'espace sur des périodes de six semaines et un an. Les modes dominants de SST montraient un déplacement spatio-temporel compatible avec la théorie récemment élaborée de la pression de facteurs éloignés (''remote forcing'') dans l'Atlantique équatorial.

Les modes dominants de la CPUE d'albacore et de listao montrent un schéma assez peu défini. Néanmoins, lorsque les modes dominants étaient calculés entre les SST et la CPUE pour les mêmes périodes et les mêmes espèces de poissons, la CPUE signalait le même déplacement spatio-temporel que les SST, à peu près à la même vitesse. Ceci indique que la prévisibilité de la CPUE est surtout due à un procédé océanographique à grande échelle, qui pourrait être associé à la pression de facteurs éloignés (''remote forcing'') dans cette région

Se estudiaron las relaciones dinámicas locales y a gran escala entre captura por unidad de esfuerzo (CPUE), para rabil y listado en el Golfo de Guinea, temperaturas de la superficie del mar (SST) y velocidad del viento. Los resultados indican porqué una determinada temperatura durante un período conduciría a una CPUE alta, mientras que en otro período conduciría a una CPUE baja. Nuestro análisis no se limitó al lugar de pesca actual.

Para obtener los datos de CPUE y de medio ambiente que faltaban, hemos utilizado un algoritmo recientemente desarrollado. Se establecieron modelos en el Golfo de Guinea para once sub-áreas separadas. Los detalles de este método se facilitan en un apéndice. Los resultados obtenidos a partir de estos modelos indican que las variables del medio ambiente estudiadas reflejan un proceso oceanográfico que comprende afloramientos y concentración de materia nutritiva, con un mes de anterioridad a una buena captura, seguida por la llegada de aguas relativamente cálidas dos semanas antes de una pesca abundante.

Se calcularon modos dominantes de variabilidad para cada parámetro en tiempo y espacio durante períodos de seis semanas y de un año. El modo dominante para SST mostró un movimiento tiempo-área que guardaba coherencia con una teoría recientemente desarrollada de ''forzamiento'' por factores remotos en el Atlántico ecuatorial.

Los modos dominantes para la CPUE del rabil y listado mostraron modelos relativamente poco definidos. Sin embargo, cuando los modos dominantes se calculaban entre SST y CPUE para los mismos períodos y especies de peces, la CPUE indicaba el mismo movimiento en el espacio y en el tiempo que el SST, aproximadamente a la misma velocidad. Esto sugería que la capacidad de pronóstico de la CPUE se debía principalmente a un proceso oceanográfico a gran escala, que podría haber estado asociado al ''forzamiento'' por factores remotos en esa zona.

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[1] This work was undertaken during a one-year sabbatical leave with the Pacific Environmental Group at Monterey, California

1. Introduction

Environmental influences on fish population dynamics are being considered increasingly important as features to understand, and to integrate, into fisheries management models (see for example, Bakun and Parrish 1980; Sharp MS). One approach to developing a basic understanding of environmental effects is to study the dynamic relations between oceanographic and meteorological patterns in time and space and those of Catch-Per-Unit-Effort (CPUE) in a particular fishery. Any such analysis assumes that CPUE is an accurate reflection of relative abundance of the fish; this may not be the case. As we will show, a considerable part of the space-time variation in CPUE may be due to changes in where, when and how much the fleet fishes, and therefore CPUE may not be a good measure of relative abundance.

Recent works on the dynamics of the eastern part of the tropical Atlantic Ocean have focused on the study of upwelling at the equator and along the north and east coasts of the Gulf of Guinea (O'Brien et al. 1978; Voituriez 1981; Picaut 1982). Based on these results, and considering that upwelling areas are favorable to the concentration and capture of tuna, we thought that it would be worthwhile to investigate the dynamic relationships between the environment and the tuna fishery, not only at the particular time and place where the tuna are caught but also in the larger space and time domains.

2. The Data Used

2.1 Environmental Data

The National Climatic Center (U.S.) routinely collects environmental data from merchant ships in the area of study. From these data files, Sea Surface Temperature (SST) and the east-west and north-south components of wind velocity were extracted and screened to eliminate bad data. The environmental data were extracted for the years 1969–1979, to coincide with available catch and effort data. As the fisheries data are available by one degree square, and by fortnight, comparable mean series were calculated for the SST data and the two wind component series. A check on the accuracy of the SST data was made by comparing the extracted series with the historical means given in the atlas by Hastenrath and Lamb (1977); when the observed value was more than three standard deviations from the mean value reported in the atlas, it was discarded from the calculations. To obtain more complete spatial coverage, SST from the historical Nansen, Mechanical Bathy Thermograph (MBT), and eXpendable Bathy Thermograph (XBT) data sets in the area were also extracted and combined with the merchant ship data. Nevertheless, the amount of data from merchant ships is greater than that in the oceanographic data file, so our spatial coverage is mostly determined by the merchant ship reports.

2.2 Fisheries Data

The fisheries data used in the study come from the French, Ivory Coast, Senegalese, and Moroccan (FISM) tuna fleets. These data, collected by the *Office de la Recherche Scientifique et Technique Outre-Mer* (ORSTOM), are by one degree square and by fortnight since 1969, and when data are not missing the following information is available:

- total catch of yellowfin, skipjack, and bigeye tuna and total effort by bait boats
- total catch of yellowfin, skipjack, and bigeye tuna and total standardized effort by medium-size purse seiners
- total catch of yellowfin, skipjack, and bigeye tuna and total standardized effort by large-size purse seiners.

The catches are reported in units of 100 kg and the effort in hours fished. We extracted from this file the total catch and effort for yellowfin and skipjack tuna, combined over the classes of purse seiners, for which the effort had been previously standardized.

3. The Spatial Grid

The oceanographic features of the eastern part of the tropical Atlantic ocean are dominated by upwelling during the winter season in each hemisphere. In the northeast part (north of 5°N), which is influenced by the climatology of the boreal hemisphere, the cold upwelled waters occur along the coast from December to May and are mainly driven by local winds and by advection. The occurrence of these cold upwelled waters is associated with a thermal front which shifts seasonally between 10°N and 20°N (Wooster et al. 1976). The southern part (south of 5°N) is influenced by the climatology of the austral hemisphere. The cold season here occurs from May to September, and upwelling occurs during this period along the equator and along both the north coast (Ivory Coast, Ghana) and the east coast (Congo, Gabon) of the Gulf of Guinea. The coastal upwelling along the north coast is separated from the open-ocean upwelling by a zone of oceanic convergence north of the equator. In contrast to the situation in the northern hemisphere, in the Gulf of Guinea the upwelling seems to be not only locally forced, but is also the result of remote forcing (Servain et al. 1982). A second upwelling of smaller amplitude occurs along the northern and eastern coasts of the Gulf of Guinea from December to January.

Taking into account these main oceanographic features and the spatial extent of the FISM tuna fleet, the eastern part of the tropical Atlantic ocean was divided into eleven large areas (Fig. 1). Dividing the region into smaller areas would have meant either too little catch and effort data in each area, or a very low density of data for the environmental parameters. After first using only eight areas in which we included large regions straddling the equator, we found we needed to have areas that were restricted to one side of the equator. (An exception is area 6. This area extends to 1° south to include the northern side of the front off Cap Lopez which is associated with the dynamics of the waters of the Bay of Biafra which are relatively warm and have low salinity). This decision meant that some areas contained fewer fisheries data than we would have preferred.

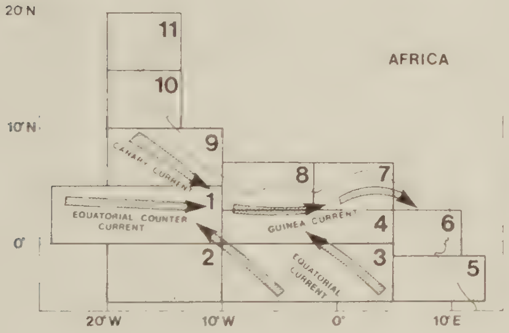


Figure 1. Spatial Grid used in this study, showing major currents in the Gulf of Guinea (after Ingham 1970)

Mean environmental and fisheries time series were calculated for each area, by fortnight, from the one degree square data. Mean CPUE was calculated as the mean of each fortnight's CPUE for each one degree square. Where there was fishing but no catch, the CPUE was defined to be zero. If there was no fishing, the CPUE was defined as missing data. The three environmental data series are missing little or no data in each area; however, the amount of missing CPUE data varies considerably among the eleven areas. The areas close to the coast have much more complete CPUE series than do the more oceanic areas, since the fleet has extended to the more oceanic areas only recently.

4. Comparison Between the Observed Time Series and the Estimated Values from the Local Models

4.1 DESCRIPTION OF THE MODELS

In the appendix we give a complete technical description of our approach to examining environmental influences in time and space on fish population dynamics. Briefly, the analysis consists of three steps: (1) estimating local (i.e. area specific) models that are used to fill in missing data points, necessary for the next two steps of the analysis; (2) calculating the dominant mode of variability in space and time of each variable, at a given frequency; (3) calculating the dominant mode of variability in space and time between two variables. In this section we examine the results of step (1).

A model of the form described in equation 1 in the appendix is estimated for each area. The model includes as variables: CPUE for both skipjack and yellowfin tuna, SST, and the north-south and east-west components of wind speed. The model is a simultaneous model in that each variable is assumed to be a linear function of all the variables of the model lagged at one and two fortnights previous to the present time period. Thus there are five equations for each area, and as the dynamics are assumed to interact, the five equations (twenty-five parameters) are estimated simultaneously. The resulting estimated parameter values are interpreted in a similar manner to multiple regression parameters.

As the results of our analyses are based on these completed time series, it is important as a first step to check how well the local models have "filled in" the missing observations. This can be done by comparing estimated and observed data when they both exist and, when there are missing data, by seeing if the estimated values agree with our qualitative knowledge of the fishery and of the environment. Further, the accuracy of the completed data was tested by artificially removing a segment of the CPUE data, treating the remaining series as the given data, then estimating the parameters of the local autoregressive models of order two (AR(2)) and the missing data points as above, and comparing the observed but artifically removed data with the corresponding estimated values produced by the model. (Only results for areas immediately relevant to the discussion are shown. Figures for all other areas are available upon request).

4.2 THE ENVIRONMENTAL DATA

The environmental time series are relatively complete except for areas 5 and 6 (not shown) where there is incomplete coverage from 1971–1972, and for area 7 where the wind data are missing for all of 1969 (Fig. 2). Where we have data, the values predicted by the model are very close to the observed values except at very high peaks in SST and wind, where the predicted values tend to be less than the observed values (an example of this can be seen in area 8, where SST in April 1971 (Fig. 3) was as high as 30.5°C while the predicted values only reach a value slightly below 30°C). Otherwise, the differences

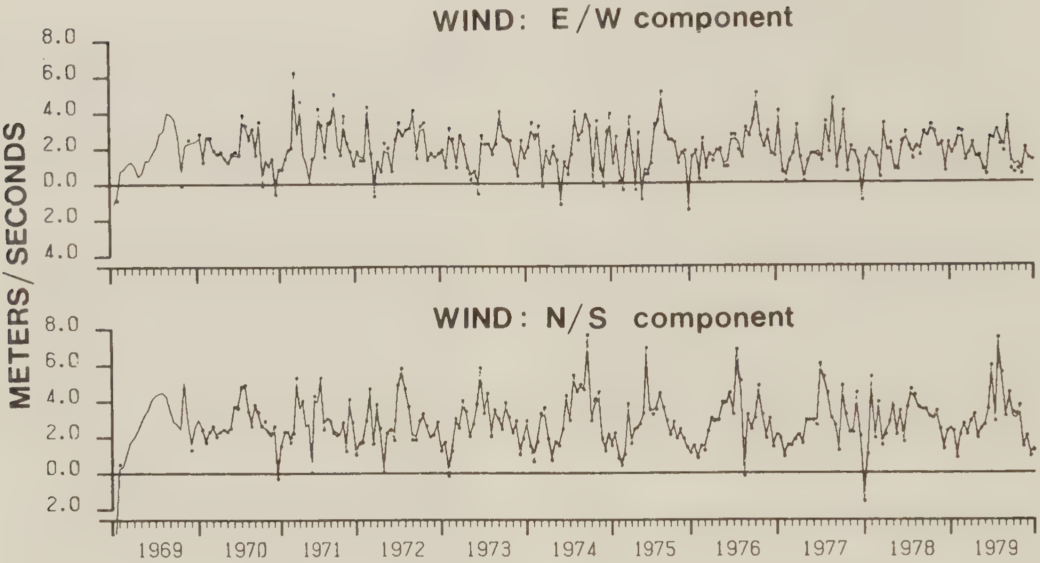


Figure 2. Observed wind speed (points connected by faint line) and wind speed predicted by the model (darker line) for area 7

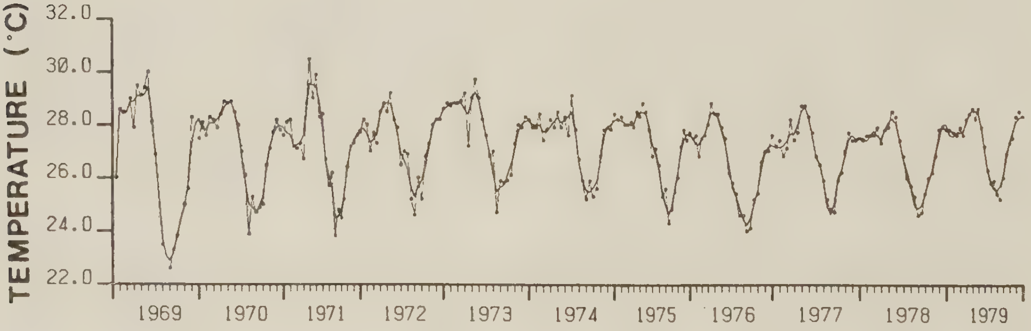


Figure 3. Observed Sea-Surface Temperatures (SST) (points connected by faint line) and those predicted by the model (darker line) for area 8.

between the observed and predicted values are barely discernible on the scale used in plotting the data.

For areas where there are many consecutive time periods with missing data, such as areas 5, 6, and 7, the predicted values again seem reasonable when we examine their qualitative properties. The predicted values during these periods of missing data are within the observed range of variation in the data, and have similar seasonal cycles as the observed part of the data (for example this is observed for area 6, from mid 1971 to early 1972). In area 7 (Fig. 2), where the wind data are missing for all of 1969, the fit seems reasonable except at the beginning of the year where there are unusually low values that are not consistent with observed values in surrounding areas. However, it is to be expected that the worst predictions would come at the beginning of the series if there are no data present, so this may partially explain the low predicted values.

4.3 The CPUE Data

In each of the eleven areas where data exist, there is very little difference between the predicted and observed values for CPUE of yellowfin and skipjack (e.g. Fig. 4). Again, the main difference appears to occur at maximum values of the peaks in CPUE. Even high frequency variations in CPUE, such as in area 5 (Fig. 4) are well predicted by the model. If there is some relationship between CPUE and the environment, this good fit is not surprising, because as the models used to complete the data were not designed to accurately forecast them, but rather to

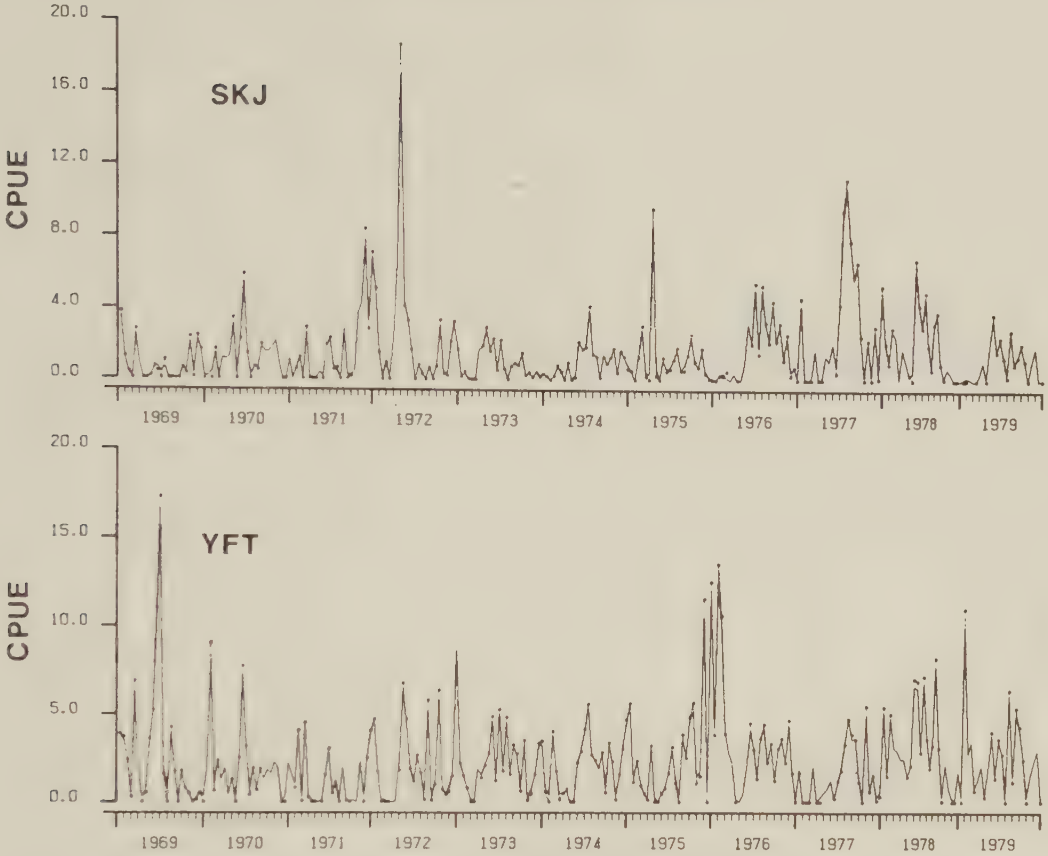


Figure 4. Catch per unit effort (CPUE) for skipjack (SKJ) and yellowfin (YFT) in area 5: observed CPUE solid points and faint line; CPUE predicted by the model, dark line

distort as little as possible the statistical properties of existing data.

When the numbers of observations of CPUE are very low, such as in areas 1, 2, and 11 (Figs. 5, 6, and 7), it is doubtful that the predicted values are quantitatively accurate. However, the predicted data may capture known qualitative properties of the fishery that would give us some reason to believe that the models reflect the actual dynamics. In area 1 (Fig. 5), the model predicts a significantly positive CPUE for yellowfin, but not for skipjack, for the last four months of 1969, 1976, 1977 and for the last two months of 1974. Examining the environmental conditions during this period, we find values slightly lower than normal, but not out of line with conditions in which tuna can survive. In 1970, 1971, 1975 and 1979 there is positive CPUE during the same part of the year and for similar environmental conditions. The data for 1980 and 1981, not used in estimating the model, show positive CPUE for both species starting in September of the year and ending around March the next year. Thus the predicted pattern of CPUE is consistent with the observed tolerances of the fish.

In area 2 (Fig. 6), the predicted values show positive CPUE for both skipjack and yellowfin between June and the first three months of the next year, with the values for skipjack being more constant. The first three months of this period correspond to the main upwelling season, when the thermocline is relatively shallow and when high concentrations of nutrients are found near the surface. Later, water masses upwelling in the eastern part of the Gulf of Guinea are drawn into this area through advection by the South Equatorial Current. Thus the environmental conditions in area 2 during this time of year do appear to be favorable for tuna. The extension of the fleet into this area in 1980 and 1981 resulted in significant CPUE for skipjack in March and April, and again in the last two months of the year. Areas 1 and 2 are also considered to be reproductive areas for skipjack (Pianet 1983; Cayré and Farrugio this volume) where this fish

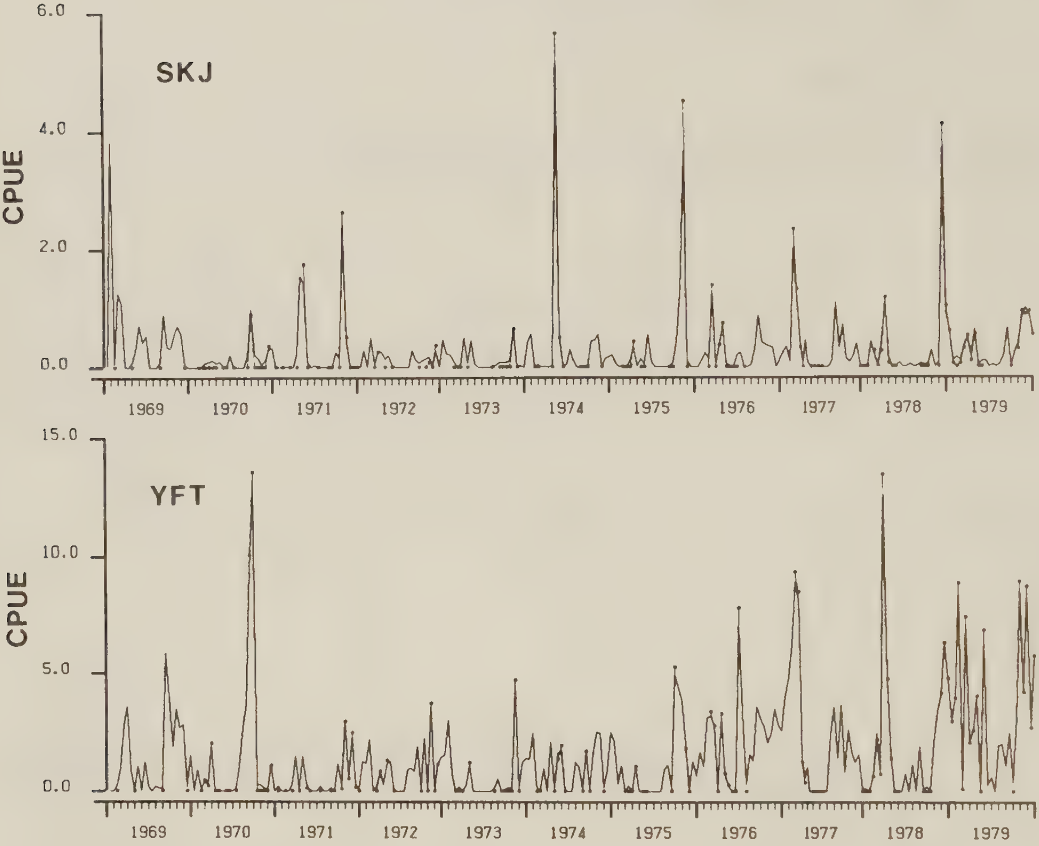


Figure 5. Catch per unit effort (CPUE) for skipjack (SKJ) and yellowfin (YFT) in area 1: observed CPUE solid points and faint line; CPUE predicted by the model, dark line.

migrates from the eastern part of the Gulf of Guinea and from the northeast region (Senegal and Mauritania) during the period from July to March of the following year.

In area 11 the fleet fishes only during the last seven months of the year, while the model predicts that there should be positive CPUE for both yellowfin and skipjack during the first five months also (Fig. 7). However, for the first four months of the year the SST values are generally below 20°C, (i.e., at temperatures where tuna are not generally encountered in this region). When fishing occurs during the last seven months of the year, the SST is at higher values, between 20°C and 28°C. As the estimated models are linear models, they will linearly extrapolate the relationship at the higher temperatures to the relationships at lower temperatures where fishing has not occurred. However, the relationship between CPUE and SST apears to have a threshold effect, and is therefore nonlinear. This is clearly a limit of our model, and cautions that the model will be most accurate when there has been at least some fishing over the entire range of the environmental variables.

Another way to test the validity of the estimation of CPUE by the AR(2) model is to remove a part of the CPUE data, to estimate the AR(2) model on the new reduced series and then to compare the estimated CPUE with the observed data not used in the estimation. This was done for CPUE data for both species in area 5. We removed the data starting from the second fortnight of May 1974 to the first fortnight of February 1975. For yellowfin the CPUE values estimated by the model were very close to the observed values (Fig. 8), showing the same three peaks as in the observed data. For skipjack, the estimated CPUE values were higher than the observed values (Fig. 8); however, if the predicted values are decreased by a constant amount the fit is quite good. This suggests that the local model is mispredicting the mean effect of the environment on CPUE for skipjack but describing in a reasonable manner the relative fluctuations. This may be because the bulk of skipjack catch is by

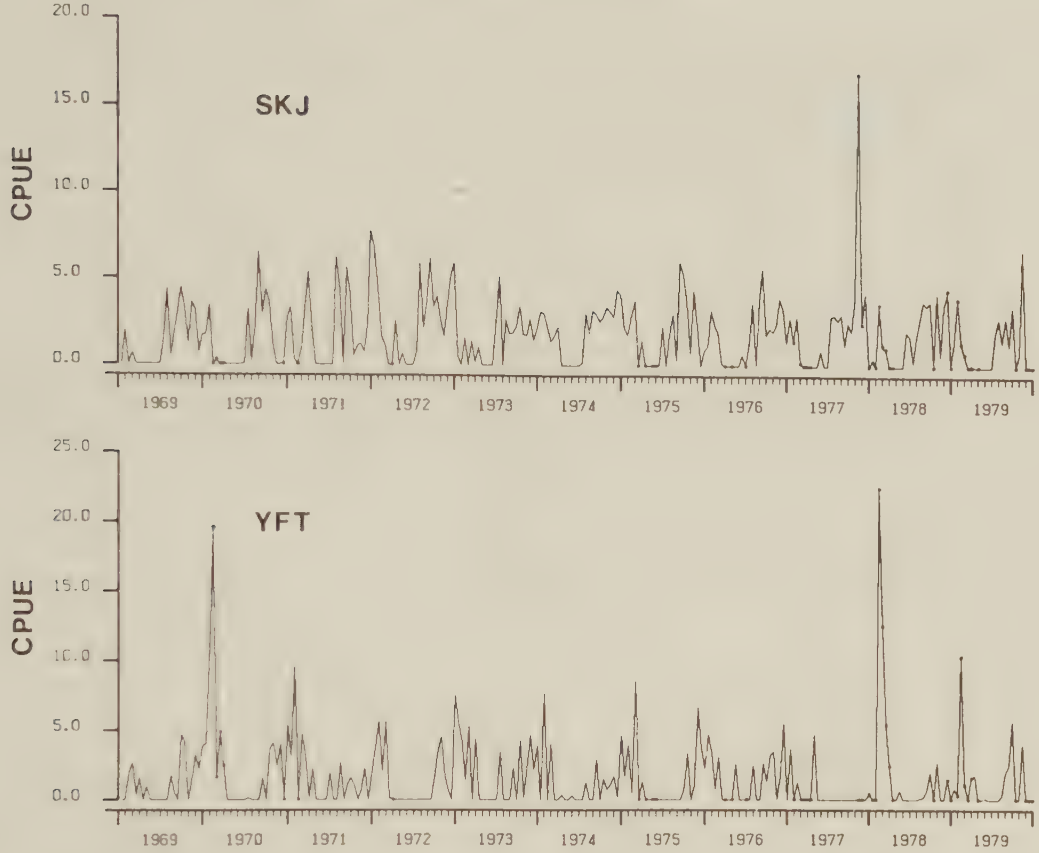


Figure 6 Catch per unit effort (CPUE) for skipjack (SKJ) and yellowfin (YFT) in area 2: observed CPUE solid points and faint line; CPUE predicted by the model, dark line

the pole-and-line fishery. Catches of skipjack by the seiners probably depends on subsurface conditions that we only indirectly describe in our models. However, the estimated values for skipjack CPUE do appear to be qualitatively reasonable.

Our ability to predict the artificially removed yellowfin CPUE data could be due to three factors: strong seasonality in the data (i.e., we are only estimating the seasonal cycle); the fact that fishing conditions tend to persist over a number of time periods; or a strong relationship between the yellowfin CPUE and the other data in the model, that is the environmental data.

The estimated spectrum for the yellowfin CPUE data in this area (not shown) essentially contains no seasonal cycle. Moreover, the ten month stretch of data have high frequency variations that are also well fitted by the data estimated by the model. Thus it seems unlikely that we are only estimating the seasonal cycle. As ten months of data have been removed, again it follows that persistence is not the explanation for the close agreement.

Thus, logically we conclude that the close agreement between the artificially removed yellowfin CPUE data and the corresponding estimated data is due to a strong relationship between the environmental variables in the model (or more likely, between oceanographic processes they represent) and the yellowfin CPUE data. This fact is confirmed when we examine the formulas and parameter values used to estimate the missing data.

5. Interpretation of the Local Models

In this section, we examine the local models used to fill in the missing data to see if we can discern a pattern that would suggest what oceanographic processes might be associated with successful fishing. This is done by examining the relative importance of each of the five variables in predicting yellowfin and

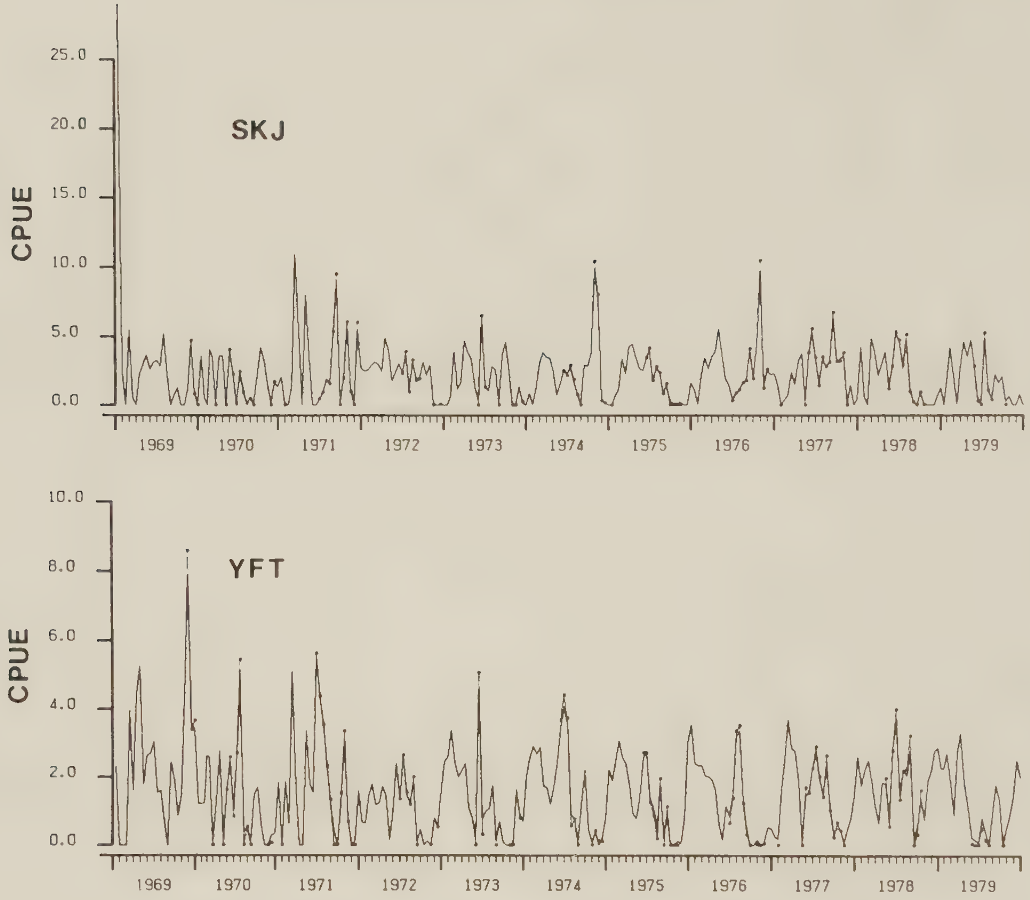


Figure 7. Catch per unit effort (CPUE) for skipjack (SKJ) and yellowfin (YFT) in area 11: observed CPUE solid points and faint line; CPUE predicted by the model, dark line.

skipjack CPUE. The most accurate way to determine the relative importance of each of the model parameters in predicting CPUE would be to standardize the coefficients by their standard errors. As discussed in the appendix, the computational burden involved precluded calculation of the standard errors. Instead we estimated the relative importance of each variable for predicting CPUE by looking at its average contribution to the predicted value, that is the relevant coefficient of Aij at time t–1 and of Bij at time t–2 times the mean of the variable in question. (For skipjack CPUE in area 1, for example, the average value for SST is 240 and the parameter at time t–1 has a value of .05 so the average contribution is .05 × 240 = 12; the north-south component of wind speed has an average value of 81 and the parameter at time t–1 has a value of –.09 for an average contribution of –.09 × 81 = –7.3. SST thus has a slightly larger average contribution.)

The estimated values of CPUE, SST and wind for all areas are given in Table 1. Figure 9 synthesizes results from the model for yellowfin and skipjack CPUE. The "SST" or "Wind" displayed in each area in the figures shows the variable(s) that were determined to be the most important, on average, for predicting the CPUE in that area (it should be noted, however, that at any particular time period a different variable may have been the most important in determining the level of CPUE for that fortnight). Also, Figure 9 shows what relative values of SST would give the largest predicted CPUE in that area. Thus, for yellowfin CPUE in area 8, the estimated value for SST one fortnight previous is 0.263 and for two fortnights previous is –0.268 (Table 1). Therefore, the model predicts a relatively larger CPUE when SST is relatively warmer one fortnight ago (to magnify the effect of the positive parameter value), and relatively cooler two periods ago (to minimize the effect of the

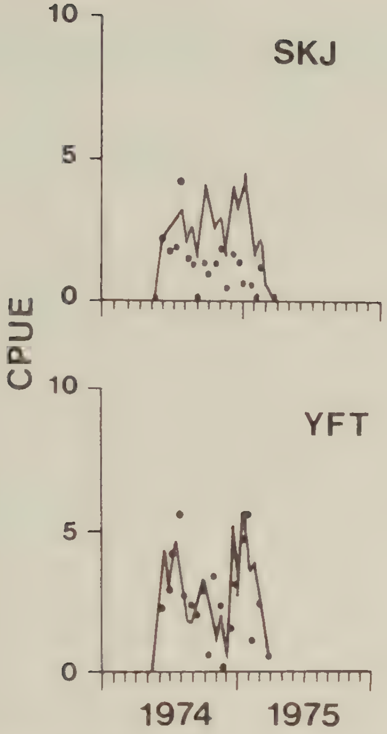


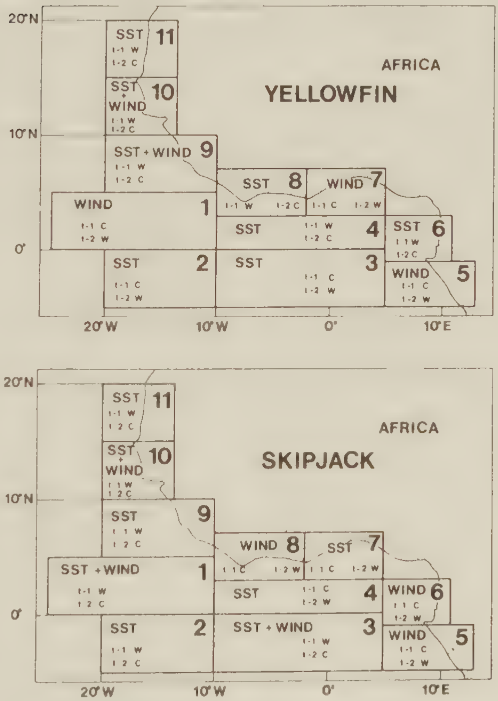
Figure 8 CPUE for skipjack (SKJ) and yellowfin (YFT) estimated by the model from the second fortnight in May 1974 to the first fortnight in February 1975 where observed data for the period was removed before fitting the model. The actual data points are indicated by the circles.

negative parameter value). This is indicated for area 8 in Figure 9 (yellowfin) by the letters SST, and W(warm) associated with t–1, and C(cold) with t–2.

The most obvious aspect of these data is that for both species, SST on the whole is the most important variable for predicting CPUE (Fig. 9). This is not surprising as many other workers have noted the association of tuna with particular water temperatures. However, having the desirable range of SST while fishing does not guarantee good catches. For yellowfin (Fig. 9), SST is the dominant or codominant factor in predicting CPUE everywhere except in areas 1, 5, and 7. Areas 5 and 7 are characterized by strong thermal fronts (at Cap Lopez and Cap Three Points) and area 1 is associated with the Guinea dome. Wind is codominant with SST in predicting CPUE in areas 9 and 10, which also are characterized by the occurrence of strong thermal fronts. For predicting skipjack CPUE (Fig. 9), wind is the dominant factor in two of the areas which are also characterized by thermal fronts (areas 6 and 8).

Another striking feature is that CPUE for yellowfin and skipjack one fortnight (t–1) and two fortnights (t–2) prior to the period under consideration is not an important contributor to the predictions. As the estimated models are simultaneous models (section 4.1), persistence of CPUE by itself is clearly not adequate to explain the observed pattern.

Another interesting pattern is observed when one looks at the coefficients for SST for each area (Table 1). The coefficients always change sign from period t–1 to period t–2, while the magnitude of the coefficients are similar at t–1 and t–2. One major grouping of ares (4, 8, 9, 10 and 11) has a positive SST coefficient one fortnight earlier and a negative SST coefficient two fortnights earlier (Table 1). According to this model, in these areas optimal conditions for high CPUE would occur if there are relatively cooler waters a month (two fortnights) ago followed by relatively warmer waters a fortnight ago. This is consistent with a physical process of colder waters richer in nutrients coming to the surface, followed and sustained by warmer waters at a sufficient


YELLOWFIN
AFRICA
SST 11 t-1 W t-2 C
SST + WIND 10 t-1 W t-2 C
SST + WIND 9 t-1 W t-2 C
SST 8 t-1 W t-2 C
WIND 7 t-1 C t-2 W
WIND 1 t-1 C t-2 W
SST 4 t-1 W t-2 C
SST 6 t-1 W t-2 C
SST 2 t-1 C t-2 W
SST 3 t-1 C t-2 W
WIND 5 t-1 C t-2 W
SKIPJACK
AFRICA
SST 11 t-1 W t-2 C
SST + WIND 10 t-1 W t-2 C
SST 9 t-1 W t-2 C
WIND 8 t-1 C t-2 W
SST 7 t-1 C t-2 W
SST + WIND 1 t-1 W t-2 C
SST 4 t-1 C t-2 W
WIND 6 t-1 C t-2 W
SST 2 t-1 W t-2 C
SST + WIND 3 t-1 W t-2 C
WIND 5 t-1 C t-2 W
20°N
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0°
20°W
10°W
0°
10°E

Figure 9. Summary of Table 1 for yellowfin (YFT) and skipjack (SKJ). In the upper corner of each area is the environmental parameter which contributes most to the predictive power of the model in that area. C (colder water) and W (relatively warmer water) in the lower corner indicate the time periods t–1 and t–2 that yield optimum CPUE.

time lag to allow the biological processes to develop, and for the occurrence of water temperatures more favorable to the immediate presence of tuna. Thus, as stated previously, the occurrence of favorable water temperatures is not sufficient to insure high abundance of tuna. The same pattern of relatively colder SST followed by relatively warmer SST is used in a model developed by Stretta and Slepoukha (1983) that determines fishing probabilities in the eastern part of the tropical Atlantic. While our models have not been tested as to their ability to forecast future levels of CPUE, we feel they are close to achieving this goal. The most difficult part, surprisingly, would be to forecast accurately the environmental conditions in a particular location. If these were known, there is some reason to believe accurate area by area forecasts of CPUE could be developed with lead times of two weeks to one month.

6. Space and Time Relationships

6.1 Single Variable Analysis

The results of step 2 of the analysis is described in this section. The data are analyzed using a technique called "Principal Components in the Frequency Domain" (PCFD). The idea is to find at each fre-

Table 1. Average contribution of five parameters to predicted value of CPUE and values of coefficients A_{ij} at time t−1, and B_{ij} at time t−2 for yellowfin (YF) and skipjack (SJ), as predicted by the model.

		PARAMETERS									
		CPUE YF		CPUE SJ		SST		WIND NS		WIND EW	
		Av. contrib.		Av. contrib.		Av. contrib.		Av. contrib.		Av. contrib.	
Area	Sp.	A_{ij} (t−1)	B_{ij} (t−2)	A_{ij} (t−1)	B_{ij} (t−2)	A_{ij} (t−1)	B_{ij} (t−2)	A_{ij} (t−1)	B_{ij} (t−2)	A_{ij} (t−1)	B_{ij} (t−2)
1		−.99		−12.68		244.10		81.66		87.64	
	YF	.3992	1377	−.3655	.3128	−.0866	.1029	− 7300	.8771	.9694	−.6667
	SJ	0273	.0371	.0824	−.1445	.0558	−.0483	−.0325	.0634	−.0974	.2862
2		13.96		4.54		234.94		57.52		32.55	
	YF	.2563	.1971	3164	.0187	−.3308	.2021	−.2007	1.3779	.5713	−.1400
	SJ	−.1157	−.0183	.3226	.2992	.0854	−.3080	−.9623	1.5594	−1.1304	−.0010
3		7.56		−3.93		219.80		27.65		20.34	
	YF	.2243	.1762	.2227	−.3026	−.5507	.3473	.7931	.8018	.2496	−.0106
	SJ	− 0559	.0421	.2943	−.0276	.0447	−.1451	−.2410	.7337	−.7090	.3203
4		12.30		−3.52		239.32		52.76		64 00	
	YF	.1001	−.0435	.3183	0668	.3665	−.3806	.5093	−.1116	.1680	.1299
	SJ	−.0257	.0005	.3472	.0838	−.1575	.1556	.0199	.0909	−.0262	.1768
5		20.99		29.69		226.29		76.74		39.12	
	YF	.1918	.1601	.1613	−.1354	−.0018	.0149	.0467	.2730	.0701	−.5037
	SJ	−.1040	−.0812	4399	.1030	−.1367	.1390	.4005	−.1027	.1210	−.1145
6		33.81		28.95		247.29		48.04		56.69	
	YF	.4177	−.1178	−.0490	.1385	.0974	−.0584	−.1118	.1840	−.0388	−.0026
	SJ	.0133	.0284	.3157	−.0216	−.0097	.0083	.0370	.1702	.0482	.1158
7		25.91		6.26		274.36		87.40		46.89	
	YF	.2493	−.0805	−.0678	.0800	−.0038	.0034	.1818	.0644	.1586	.0575
	SJ	.1999	−.1732	.2483	−.0458	−.1217	.1444	.0289	.0090	1607	−.1864
8		69.09		−1.79		203.00		94.16		53.48	
	YF	.3208	−.0788	.2805	−.0324	.2630	−.2676	.2786	−.0269	−.0088	.1598
	SJ	.0013	.0087	.5067	−.0519	−.0087	.0065	.0687	.0170	−.0669	.1352
9		−23.99		21.18		265.80		.98		16.73	
	YF	.2497	−.0314	.0088	.0761	.0469	−.0377	−.1131	−.0879	−.3317	1.2914
	SJ	.0371	−.0743	.1700	.0946	.2309	−.2123	.0323	−.0331	−.7241	.7539
10		17.70		15.97		235.96		36.16		23.78	
	YF	−.0048	.0553	.2269	−.0552	0660	−.0679	−.5808	.4520	.4996	−.0383
	SJ	−.0933	−.0695	.4325	−.0400	.0390	−.0088	.0389	.0032	.1395	.0591
11		−3.62		−1.67		203.21		21.89		56.42	
	YF	.2937	.0845	−.0799	−.2876	.1215	−.1195	−.2366	− 0595	.0970	−.1214
	SJ	−.7382	.4539	.4420	−.0344	.9800	−.8695	.3106	−.0679	1.3241	−1.9779

quency the dominant mode of variation in the data. That is, at each time period we form a one-dimensional time series by taking a linear (weighted) combination through time of the relevant data series for the eleven areas that have the property of containing the most spectral variance at all frequencies compared to any other such combination. Thus the new series at any time period t is a linear combination of the eleven areas at period t, plus another linear combination of the eleven areas at time t−1, and so forth.

The new component series is an artifice, and acts as a reference point. As we calculate the relevant weights in the frequency domain, we can calculate the coherence (the spectral equivalence of correlation) and phase between any of the original series and the component series at any frequency. The coherence tells us how much of the spectral variance of any original series (at a given frequency) is contained in the component series, that is how well the component series reflects the dynamics of a given area.

The phase tells us by how much any original series lags behind the component series (at a given frequency). As the component series is an artifice, we have in effect calculated the relative lags between all eleven areas (at a given frequency). As the eleven series are distributed in space, and the lags are in time, this gives us a description of the dominant space-time dynamics (at a given frequency). Thus, the results to be presented show the dominant space-time dynamics of a variable at a given frequency. At the annual frequency, this would be like showing the dominant "average" dynamic that takes one year to occur, rather than the dynamics of any particular year, just as a regression line describes "expected" or "average" behavior.

6.1.1 Analysis of the SST data

In the tropical Atlantic ocean, the amplitude of the seasonal cycle of SST is several times greater than that of the interannual variability (Merle et al. 1980). A fourier decomposition of both the SST data and of thermal structure data has shown that the seasonal cycle is mainly composed of the first two harmonics, annual and semi-annual (Merle and Le Floch 1978).

For this reason, we describe our results for frequencies centered at periods of twenty-two and eleven fortnights. These correspond to the annual and semi-annual frequencies in our data. Only the first, or dominant *eigenvector* is discussed for each frequency, because at each frequency this component contains the predominance of the spectral variance (90%). As described in the appendix the phases are calculated by arbitrarily giving the dominant component a phase of zero with area 4.

For a period of twenty-two fortnights (Fig. 10), the coherence between the dominant principal component and each of the areas is very high except in area 9, off Sierra Leone. Area 9 is the meteorological equator (or atmospheric thermal frontier between the two hemispheres) and is affected by the bi-annual oscillations of the Inter-Tropical Convergence Zone, inducing a strong bi-annual oscillation in the SST data. When we look at the phase relations of the SST at this frequency, we see a decomposition of this part of the Atlantic into two parts; a northern part (area 10, 11) separated from the southern part by area 9. The phases in these two areas differ by roughly eleven fortnights (six months), which corresponds to the delay between the seasonal cycles of the two hemispheres.

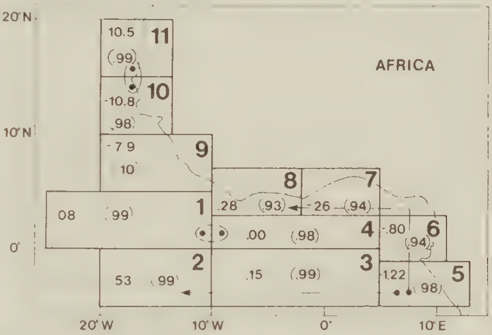


Figure 10. Phase and coherence (in parentheses) of SST between the eleven areas at twenty-two fortnights and for the first component of the *eigenanalysis*. The phases are in units of fortnights. The arrows represent our interpretation of the phase lag progression. Areas in phase are noted by encircled pairs of dots

The southern part shows an interesting spatial pattern in the phase relationships at this frequency. Our interpretation of this pattern is based on a theory of remote forcing in the Gulf of Guinea (O'Brien et al. 1978). In this theory, the main upwelling in the Gulf of Guinea is believed to be caused by a Kelvin wave generated by an increase of the zonal wind stress in the western part of the Atlantic basin. This wave then propagates along the equator to the eastern part of the basin, and then poleward along the northern and southern coasts of west Africa, inducing a movement of the thermocline towards the surface. In Figure 10, we see that the equatorial areas north of the equator are in phase. Along the Gulf coast, from areas 6 to 8, the phase lag between areas is relatively constant (approximately 0.4 fortnight) and is consistent with the estimated speed of a Kelvin wave (1½–2 m/sec compared to a theoretical 3 m/sec). The phase lag between area 5 and area 6, however, shows movement from south to north that is not consistent with a Kelvin wave. To completely resolve this question, we need to extend the study area farther south. However, a more detailed analysis of the SST data, to be described elsewhere, lends further support to the Kelvin wave theory. The two oceanic areas south of the equator have phase lags which show a westward movement of water apparently related to advection by the South Equatorial Current.

At the higher semi-annual frequency (Fig. 11) all the areas are highly coherent with the dominant principal component, except for area 11. The two equatorial areas north of the equator are still approximately in phase. As for the annual frequency, we again find phase lags which suggest a movement of water from area 6 to 8, but at these frequencies the movement extends to area 10. This extension at the semi-annual periods is consistent with our previous discussion about area 9 being the meteorological equator dominated by semi-annual frequencies. Also the oceanic areas south of the equator exhibit a westward movement of water similar to that at the annual frequency. Significant six month signals have been found in the subsurface thermal structure (Merle and Le Floch 1978), in sea level data (Verstraete et al. 1980), and in the wind and coastal station data (Picaut et al. 1978). Therefore, there is good reason to believe that the observed behavior at a period of six months is not just due to a simple harmonic of the annual cycle. The second upwelling event, which occurs south of the equator in December and north of the equator in January, also suggests that the semi-annual behavior is not simply a harmonic. The same kind of propagation of the SST signal has been demonstrated to occur along the northern and southern coasts during the main upwelling period by Picaut (1982), and along the coasts of Ghana and the Ivory Coast during the second upwelling period by Roy (1981).

6.1.2 Analysis of CPUE data

The dominant mode of variation displayed by the CPUE data for both yellowfin and skipjack at the periods of interest (eleven and twenty-two fortnights) does not present as clear a picture as does the SST data. At many frequencies it is not clear that the variations in CPUE represent anything more than fleet dynamics. For example, at a period of twenty-two fortnights (Fig. 13) the dominant pattern of CPUE for yellowfin appears to be a movement in the CPUE from area 8 down to area 1 and 2, and from area 10 to area 11 and 9, which is consistent with fishing behavior of the fleet from one of the ports. Skipjack CPUE especially shows little pattern, with the highest coherences at most frequencies occurring in the areas adjacent to the major ports.

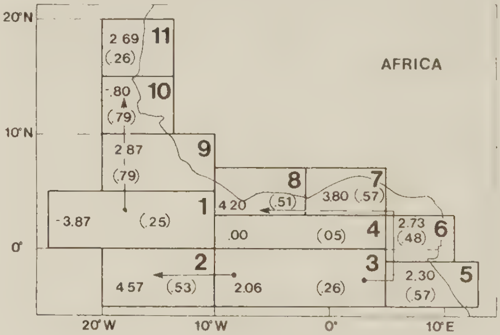


Figure 12. Phase and coherence (in parentheses) of CPUE for yellowfin between the eleven areas at eleven fortnights and for the first component of the *eigenanalysis*. The phases are in units of fortnights. The arrows represent our interpretation of the phase lag progression.

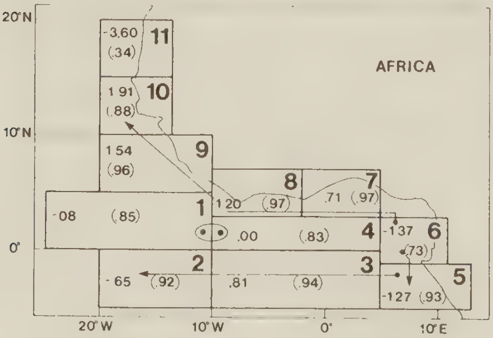


Figure 11. Phase and coherence (in parentheses) of SST between the eleven areas at eleven fortnights and for the first component of the *eigenanalysis*. The phases are in units of fortnights. The arrows represent our interpretation of the phase lag progression. Areas in phase are noted by encircled pairs of dots.

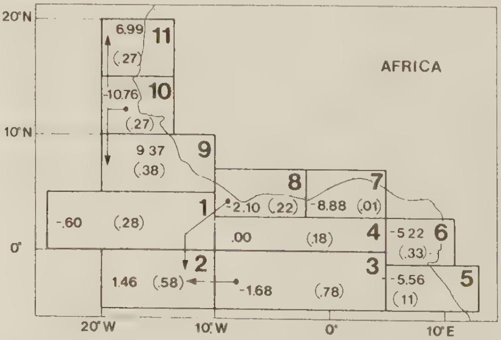


Figure 13. Phase and coherence (in parentheses) of CPUE for yellowfin between the eleven areas at twenty-two fortnights and for the first component of the *eigenanalysis*. The phases are in units of fortnights. The arrows represent our interpretation of the phase lag progression.

6.1.2.1 Yellowfin CPUE: At a period of eleven fortnights (Fig. 12) the yellowfin CPUE shows a fairly regular propagation northward along the coast from area 5 to area 6 to area 7 to area 8. This is consistent with one part of the dominant pattern in the SST's, and suggests the association of the arrival of tuna with the proper water temperatures (a question to be explored more fully in the next section). Also, at a period of 14.67 fortnights, there appears to be a steady progression northward from area 9 to area 10 and to area 11.

6.1.2.2 Skipjack CPUE: There appears to be little pattern in the skipjack CPUE except for close association with the major ports. Only at a period of eleven fortnights (Fig. 14) is there any pattern. Here we see a fairly regular propagation from area 1 to area 9, from area 11 to area 10 and to area 9, and from area 4 to 6, to 5 and to 3. The last feature suggests that fishing occurs along entrained upwelling waters, as discussed previously. The southwest propagations from area 11 to 9 could be related to the development of the thermal front associated with upwelling.

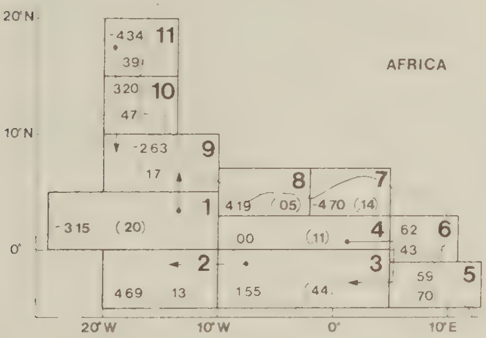


Figure 14. Phase and coherence (in parentheses) of CPUE for skipjack between the eleven areas at eleven fortnights and for the first component of the *eigenanalysis* The phases are in units of fortnights. The arrows represent our interpretation of the phase lag progression.

What is most notable is that there appears to be relatively little understandable pattern to the dominant modes of variation in the CPUE data. As we will see in the next section, the situation changes dramatically when CPUE is analyzed in conjunction with SST. Thus this lack of pattern in the CPUE data is significant for two reasons: it underscores the importance of the environmental features, and it reinforces the need to look at each variable individually before examining a variable in conjunction with a second variable.

6.2 Analysis of Two Variables Over Space and Time

In this section, we examine the results for step 3 of our analysis. As in step 2, we work in the frequency domain, and as in step 2 we will form a one-dimensional component series that is a linear combination through time of the relevant variable measured at each of the eleven areas. However, the criterion for selecting the linear combinations is different. As we want to examine the influence in space and time of one variable on a second variable, we will be looking for the linear combinations through time of each variable that are the *most coherent* at all frequencies, rather than the linear combination that explains the most spectral variance at all frequencies.

In section 5, we presented evidence that CPUE for tuna in the Gulf of Guinea is strongly influenced by the presence or absence of particular environmental conditions. However, that analysis does not tell us if the relationship is mainly a local one, in which case there is little added predictive capability from knowing what is happening in the entire Gulf, or if the strong relationship is due to a broadscale process, in which case spatial patterns will be as important as temporal patterns in making predictions.

This analysis was performed for yellowfin and skipjack CPUE with SST as the second variable. The one-dimensional series formed by the analysis are called the *canonical series*. As before, we can calculate the phase and coherence between any original series and the corresponding canonical series (at a given frequency).

The most obvious feature of this analysis is that the pattern of propagation shown by SST is very similar to the pattern when SST is analyzed alone (compare e.g. Figs. 12 and 15). At periods of both eleven and twenty-two fortnights, we see the fairly regular propagation of SST along the coast (Figs. 15 and 16; 17 and 18), as well as a westward propagation of SST in the oceanic areas south of the equator. At a period of twenty-two fortnights (Figs. 16 and 18), we again see

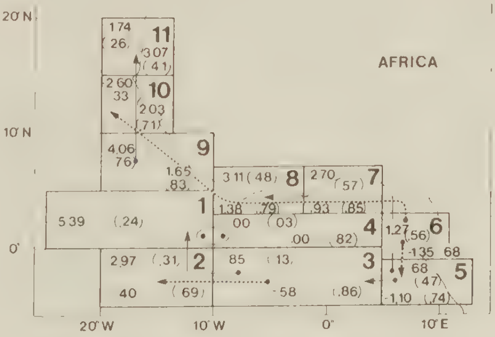
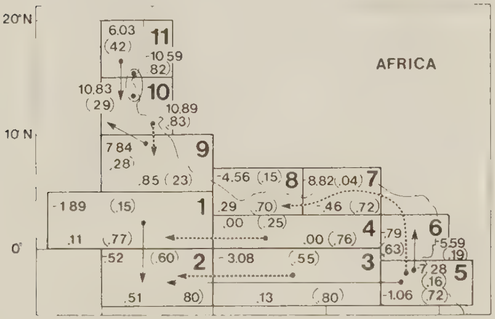


Figure 15 Phase and coherence (in parentheses) of CPUE for yellowfin (upper corner) and SST (lower corner) between the eleven areas at eleven fortnights and for the fixed components of the canonical analysis. The phases are in units of fortnight The arrows represent our interpretation of the phase lag progression for yellowfin (solid line) and for SST (dashed line). The areas in phase are denoted by encircled pairs of dots

for the two species that the northern regions are roughly six months out of phase with the southeastern regions. The importance of this observation is that this is the part of the SST data at these frequencies that is most coherent (coherences are all 0.9 or greater) with the CPUE data. This is very strong evidence that the evolution of CPUE for both skipjack and yellowfin in the Gulf of Guinea is closely related to the evolution of SST at the same frequencies. If we examine the phase relationships at a period of twenty-two fortnights in the yellowfin CPUE canonical series (Fig..16), it is clear that except for area 7, where the coherence is low (0.04) the yellowfin CPUE data show the same spatial evolution in time along the eastern coast as does the SST canonical series. For the skipjack CPUE data (Fig. 18), the pattern is not as clear at this frequency.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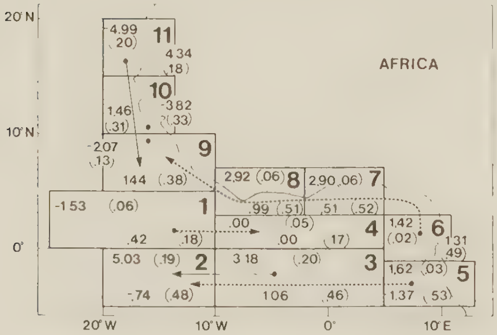
2
3
5
6.03 (42)
-10.59 (.82)
10.83 (29)
10.89 (.83)
7.84 (.28)
.85 (23)
-4.56 (.15)
8.82 (.04)
-1.89 (.15)
.29 (.70)
.46 (.72)
.00 (.25)
.11 (.77)
.00 (.76)
.79 (.63)
5.59 (.19)
.52 (.60)
-3.08 (.55)
7.28 (.16)
.51 (.80)
.13 (.80)
-1.06 (.72)

Figure 16. Phase and coherence (in parentheses) of CPUE for yellowfin (upper corner) and SST (lower corner) between the eleven areas at twenty-two fortnights and for the fixed components of the canonical analysis. The phases are in units of fortnight. The arrows represent our interpretation of the phase lag progression for yellowfin (solid line) and for SST (dashed line) The areas in phase are denoted by encircled pairs of dots.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10
9
8
7
1
4
6
2
3
5
4.99 (.20)
4.34 (.18)
1.46 (.31)
-3.82 (.33)
-2.07 (.13)
1.44 (.38)
2.92 (.06)
2.90 (.06)
-1.53 (.06)
.99 (.51)
.51 (.52)
.00 (.05)
.42 (.18)
.00 (.17)
1.42 (.02)
1.31 (.49)
5.03 (.19)
3.18 (.20)
1.62 (.03)
-.74 (.48)
1.06 (.46)
1.37 (.53)

Figure 17. Phase and coherence (in parentheses) of CPUE for skipjack (upper corner) and SST (lower corner) between the eleven areas at eleven fortnights and for the fixed components of the canonical analysis. The phases are in units of fortnight. The arrows represent our interpretation of the phase lag progression for skipjack (solid line) and for SST (dashed line). The areas in phase are denoted by encircled pairs of dots

At a period of eleven fortnights, again yellowfin CPUE and SST have remarkably similar patterns and speed of movement (Fig. 15). For skipjack CPUE and SST at this frequency, the coherence is low along the eastern coast and for the two oceanic areas north of the equator. Along the northern coast (area 11, 10, 9) the CPUE shows a regular movement from area 11 to 10 and to 9.

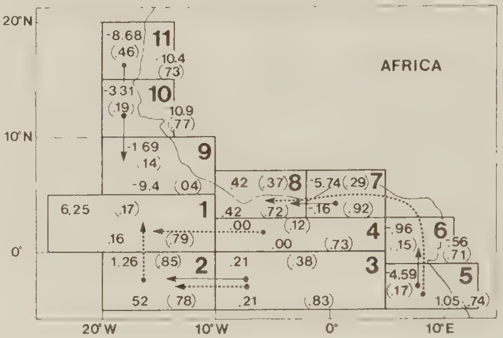
20°N
10°N
0°
20°W
10°W
0°
10°E
AFRICA
11
10
9
8
7
1
4
6
2
3
5
-8.68 (.46)
-10.4 (.73)
-3.31 (.19)
10.9 (.77)
-1.69 (.14)
-9.4 (.04)
.42 (.37)
-5.74 (.29)
6.25 (.17)
.42 (.72)
.16 (.92)
.00 (.12)
.16 (.79)
.00 (.73)
.96 (.15)
.56 (.71)
1.26 (.85)
.21 (.38)
4.59 (.17)
.52 (.78)
.21 (.83)
1.05 (.74)

Figure 18. Phase and coherence (in parentheses) of CPUE for skipjack (upper corner) and SST (lower corner) between the eleven areas at twenty-two fortnights and for the fixed components of the canonical analysis. The phases are in units of fortnight. The arrows represent our interpretation of the phase lag progression for skipjack (solid line) and for SST (dashed line). The areas in phase are denoted by encircled pairs of dots.

As mentioned in an earlier section, the phase relationships only have meaning for a single variable across areas. A more precise discussion of these results would require calculating the phase lag between the two canonical series, so that we can better determine the timing between the propagation of SST and of CPUE. However, what is remarkable is that while the dominant modes of variation for CPUE alone show no consistent pattern, when analyzed simultaneously with SST data, the most predictable parts of the CPUE data exhibit very clear patterns of movement. The propagation of SST, coherent with the CPUE, appears to be related to the occurrence of upwelling along the coast in the Gulf of Guinea, and with advective processes in the oceanic and northern parts of the Gulf. Thus from a physical viewpoint, it is not surprising that the CPUE data should show an evolution similar to the SST propagation, as the regions with upwelling waters have an enrichment of food that is favorable for the aggregation of tuna.

7. Summary and Conclusions

In this paper we have studied both the local and the broadscale dynamic relationships between CPUE for yellowfin and skipjack tuna in the Gulf of Guinea with SST and with wind speed. It is not our purpose to review past work on environmental influences on tuna catches. Good reviews can be found in Blackburn (1965) and Sund et al. (1981). What separates our work from any of the papers referenced in those two works is that first, we truly analyze the dynamics of the relationships, rather than just the mean habitat where high levels of CPUE occur. This allows us, for example, to explain why a particular temperature during one time period will lead to high CPUE while the same temperature conditions will lead to low CPUE at other times. Moreover, our analysis is not restricted to where fishing has actually occurred; if we are ever to forecast where good fishing will occur the only information available will be present environmental conditions and past fishing success. The forecast must be able to distinguish, for example, fronts that will have tuna aggregated and fronts that won't, *before fishing occurs*. To our knowledge our models are the first to directly tackle this problem.

In more detail, an examination of our local models shows that CPUE for both species of tuna is primarily estimated by the evolution of the environmental conditions, rather than from either persistence of fishing conditions or by the present environmental conditions. The "scenario" used by the models is consistent with known direct observations at sea. This "scenario" predicts higher concentrations of tuna when there has been upwelling one month previous to fishing followed by a relative warming of the waters two weeks previous to the fishing. This suggests that the predicted relationship is only a surrogate for a more complicated evolution of biological and physical processes which results in areas favorable for the aggregation of tuna.

The local models suggest that there are broad areas with similar behavior, and that these areas correspond to areas with similar oceanographic dynamics. To examine this further, we used a technique that allows us to study the dominant dynamics of one or two variables in both space and time and at a given frequency. This analysis reveals little pattern when CPUE is analysed by itself, but when CPUE is examined with SST we find the two variables moving in a similar pattern with a similar speed of movement. The pattern found is identical to the pattern found for SST when it is analyzed by itself, and is consistent with a theory of remote forcing in the region. This suggests that fishing conditions also are associated with the remote forcing, and that forecasting of CPUE could be enhanced by using both broadscale and local environmental conditions. The relationship to remote forcing is an entirely new result, and emphasizes the importance of not limiting studies of the relationships between CPUE and the environment to locations and times where fishing occurs.

In this study, we only used surface environmental parameters. It would be interesting and instructive to introduce some properties of the vertical structure as well. For example, the depth of the thermocline would be an important parameter to consider, because the variation of the vertical habitat of the fish and the vulnerability of the fish to surface fishing gear is related to the vertical temperature structure. However, subsurface data tends to be much sparser than surface data.

This study examines the influence of the environment only after the recruitment phase; at this stage of the life-history of pelagic fish environmental effects are not a dominant factor for the survival of the fish, but rather tend to affect the ability of the fish to aggregate and to be available to a surface fishery. Before the recruitment phase, the environment could be the dominant factor for the survival of the stock. The success of reproduction and the survival of larvae may be controlled by advective or transport processes (Parrish et al. 1981).

A curious feature of our results is the fact that none of our models directly includes recruitment. This suggests that either we have somehow indirectly modelled recruitment (unlikely), or that recruitment during the period of study has been steady, perhaps fluctuating around a mean level, or else that the fishery during the period of study has not been limited by the population size. Studies of the relationships between the environment and the larval and juvenile stages of the tuna would be necessary to help clarify these issues.

Acknowledgements

Support for one of the authors (Cl. R.) was provided through a cooperative agreement between NMFS and ORSTOM during a visit to the Pacific Environmental Group, Monterey, California. We wish to express our gratitude for the many hours of assistance rendered by Craig Nelson in preparing the data for our calculations and in reviewing the manuscript. This study has also benefited from an efficient preparation of the raw data by Jean Jacques Le Chauve and Daniel Corre of ORSTOM, Brest, France, and from detailed comments of an anonymous reviewer.

Appendix

Methods and Assumptions of the Data Analysis

A.1 The Basic Problems

There are three main problems to be dealt with when trying to analyze the tuna CPUE and environmental data from the Gulf of Guinea. These are: (1) the sheer size of the problem, (2) missing data in the time series, and (3) resolving time and space relationships among several variables at once. We will briefly discuss each of these problems. First, as described in the preceding sections, we want to examine the interrelationships among five different variables at eleven locations. If each variable in each area is treated as a separate time series, then we would be directly modelling fifty-five time series. In this case, even a simple model of the form $X_t = AX_{t-1} + e_t$ would require estimating 3025 parameters in the coefficient matrix A, which clearly is impractical.

Second, only a few of the fifty-five time series have no missing data points. While the environmental data are fairly complete, the CPUE time series have many missing values, because there are no data for an area at any time during which there was no fishing in that area. This clearly is a problem if we consider CPUE as a measure of relative abundance. The absence of fishing does not necessarily mean the absence of fish, and when studying the space-time dynamics the most consistent estimate may well be that there were fish in the area and therefore, that a positive CPUE would have been possible.

The third problem is to resolve behavior in both time and space among several variables. For the problem at hand, there are good a priori reasons to believe that standard assumptions such as isotropy are not valid; indeed it is not obvious that any of the variables even satisfy the weaker assumption of spatial stationarity. Thus we must find a method of analysis that can deal with the large size of the problem without imposing on the data any assumptions of spatial stationarity.

A.2 Estimating Missing Values

To "complete" the missing data, we elected to construct local multivariate time series models in each area, simultaneously modelling the five variables of interest. We will use the following notation:

$Y(t) = (Y_1(t), Y_2(t))^T$ = column vector of yellowfin and skipjack CPUE in time period t.

$X(t) = (X_1(t), X_2(t), X_3(t))^T$ = column vector of SST, N–S, and E–W components of wind velocity.

where ^{T} denotes matrix transpose. The model estimated in each area is a second-order multivariate autoregressive model (AR(2)) of the form:

$$\begin{pmatrix} Y(t) \\ X(t) \end{pmatrix} = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix} \begin{pmatrix} Y(t-1) \\ X(t-1) \end{pmatrix} + \begin{pmatrix} B_{11} & B_{12} \\ B_{21} & B_{22} \end{pmatrix} \begin{pmatrix} Y(t-2) \\ X(t-2) \end{pmatrix} + E_t$$

$$\begin{pmatrix} U(t) \\ V(t) \end{pmatrix} = \begin{pmatrix} H_1(t) \\ H_2(t) \end{pmatrix} \begin{pmatrix} Y(t) \\ X(t) \end{pmatrix} + W_t \qquad (1)$$

where A and B are 5 × 5 matrices of parameters to be estimated, E_t is a 5-vector of independent Gaussian random variables with mean mu and covariance matrix Σ, W_t is the vector of observation noise, a random gaussian vector of mean zero and covariance matrix R, H(t) is a matrix of known parameters, and U(t) and W(t) are the noisily observed data series. The matrix H(t) can be used to signify that a series has a missing data point in time period t.

There are several reasons for choosing a model of the form (1). First, as most of our analysis will consist of spectral methods, the major goal in completing the time series is to cause minimal distortion of the covariance structure of the observed data. AR(2) models offer a flexible class of models that can closely approximate many different types of spectra. Typical AR(2) spectrums exhibit a small peak in the low frequency band. As most of our data are dominated by a seasonal cycle with a period of twenty-four fortnights, we would expect the actual spectrum to have a similar peak. Thus the data estimated from the AR(2) models should provide reasonable spectral estimates, but somewhat smoother (particularly at higher frequencies) than if the real data were available.

Ideally, both for more accurate estimates and for better forecasting models, some rigorous order determination method would be used to select the "best" AR model for each area, and all nonsignificant parameters would be set to zero. This approach was precluded by the already considerable computational burden (fifty iterations of the estimation routine require one hour of CPU time on a CDC 6500) and the fact that the information matrix, necessary for assessing the precision of the parameter estimates, can only be estimated numerically and requires substantially more computational time. Thus the AR(2) models would seem to give a reasonable tradeoff between computational burden and distortion of the covariance structure of the data.

Major reasons for choosing AR models are: (1) they are biologically reasonable, (2) they can be interpreted easily, and (3) there exists an algorithm (Shumway and Stoffer 1982) for exact maximum likelihood estimation of AR models when there are missing data, using Kalman filtering and the E–M algorithm (Dempster et al. 1977). This is an iterative algorithm that starts with initial guesses for the parameters, calculates minimum mean square error estimates of the missing data, and then calculates maximum likelihood estimates of the parameters using the completed data set. The next iteration then begins by computing new minimum mean square error estimates for the missing data, using the latest parameter estimates. The algorithm converges when the completed data set produces maximum likelihood estimates of the parameters sufficiently close to those found in the previous iteration. Thus at convergence, the completed data sets yield maximum likelihood estimates of the particular parameters, and the estimated parameters give minimum mean square error of the missing data. Details of the algorithm can be found in the paper by Shumway and Stoffer (1982).

Models that also include information from neighboring areas probably would produce more accurate estimates of the missing data. We did not choose to do this for two reasons. First, the resulting models would have a large number of parameters to estimate compared with the number of time periods in our data. Second, including neighboring areas in the fill-in models could bias our findings on space-time behavior. By restricting ourselves to local models to fill-in the missing data, we feel more confident that any spatial relationships found are not artifacts. *A posteriori*, this appears to have been a wise decision, as the local models have many desirable properties and capture many known qualitative features of the eleven areas. Hence, it is doubtful that there was much to be gained from estimating the missing data using much larger models.

Spectral density matrices were calculated for the completed time series for frequency bands centered at intervals of 0.02273 cycles per fortnight. The spectral densities were estimated by Fourier transformation of the completed data series and by direct smoothing of the periodogram, as in Brillinger (1981, chapter 7). A bandwidth of 0.02273 gives thirteen degrees of freedom. While a larger bandwidth would give more precise estimates, it would no longer be possible to resolve interannual frequencies. Also, graphs of some of the series suggest there may be cyclic behavior at 2⅓ to 3 years. However, smaller bandwidths were not used to resolve these frequencies because the resulting degrees of freedom were too few. The spectral density matrix for the CPUE at frequency will be denoted by fyy(λ) (or fyy where the frequency is either obvious or irrelevant) and the spectral density for the environmental series by fxx(λ) (or) (fxx). The cross-spectral densities are denoted by fyx(λ) (or) (fyx) and fxy(λ) (or) (fxy) where fyx = fxy* and * denotes conjugate transpose.

A.3 ANALYZING A SINGLE VARIABLE IN TIME AND SPACE

In order to be able to understand and interpret the space-time variations of two variables together, it is necessary to understand the dominant mode of variation in each series separately. This gives us a clearer picture of the dynamics in each variable, and how they change when analyzed simultaneously with a second variable.

Suppose we have an r-vectored valued second-order stationary series X(t) with mean zero and covariance function Cxx(μ). Further, suppose we wish to find a q-vector valued series Y(t) with q<r such that:

$$Y(t) = \sum_{\mu} b(\mu)\, X(t-\mu) \tag{2}$$

i.e., Y(t) is a filtered version of X(t) such that Y(t) is close to X(t) in the sense that we minimize:

$$E\left\{[X(t) - \sum_{\mu} c(t-\mu)\, Y(t)]^{T}[X(t) - \sum_{u} c(t-\mu)\, Y(t)]\right\} \tag{3}$$

where c(μ) is the inverse filter.

It is proven in Brillinger (1981, chapter 9) that the solution to this problem is given by the filter:

$$\begin{aligned} b(u) &= 2\pi \int_{-\pi}^{\pi} B(\alpha) \exp(i\alpha u)\, d\alpha \\ c(u) &= 2\pi \int_{-\pi}^{\pi} D(\alpha) \exp(i\alpha u)\, d\alpha \end{aligned} \tag{4}$$

where,

$$B(\lambda) = \begin{bmatrix} V_1^* \\ \cdot \\ \cdot \\ \cdot \\ V_q^* \end{bmatrix} \quad \text{and } D(\lambda) = B(\lambda)^*$$

and the vector $V_k(\lambda)$ is the k-th eigenvector of the matrix fxx(λ) associated with the eigenvalue $m_k(\lambda)$. In practical terms, the solution to (3) is found by calculating the principal components of the complex matrices fxx(λ) at all frequencies. It is not necessary to calculate the inverse transforms (4), as it is possible to calculate the gain, coherence, and phase between the original series and each principal component series (Brillinger 1981; Michaelson 1982a). At any given frequency, the coherence tells us how much of the spectral variance of the original series at this frequency is contained in the component series, and as the component series can be arbitrarily set to have zero phase with any area, they act as fixed reference points to determine the time relationships between the part of each original series contained in the component. Principal components in the frequency domain have been used extensively by Michaelson (1982a, 1982b) and earlier by Wallace (1972) and Wallace and Dickinson (1972).

Principal component analysis has been used extensively in oceanography under the name "Empirical Orthogonal Function" (EOF) analysis. The difference between EOF's and the present analysis is that, in comparison to (2), EOF's are restricted to a transform of the form $b_0X(t)$. Equivalently, if we were to smooth our spectral estimates over all frequencies, then the two analyses would be equivalent (Brillinger 1981, chapter 9). Also, principal components analysis in the frequency domain produces q series that are independent at all frequencies, and hence at all lags, which is not true of EOF's. Further, the phase relationships at each frequency are readily available from this method, while EOF's would require extensive further calculations to obtain any kind of comparable results.

A.4 ANALYZING TWO VARIABLES IN TIME AND SPACE

At first glance, a method for dealing with two sets of variables would be to extend the previous analysis to the matrix

$$\begin{bmatrix} f_{xx}\, f_{xy} \\ f_{yx}\, f_{yy} \end{bmatrix}$$

However, this is not appropriate for several reasons. First, principal component analysis is scale sensitive, and the two sets of variables may be measured in units that greatly differ in magnitude. Second, if we were to look at the linear combination of the first set of variables on the dominant component and the linear combination of the second set of variables also on the dominant component, even though this component contains the greatest total variance, it is not necessarily true that these two linear combinations will be very coherent. Since in dealing with two sets of variables we are interested in discovering related dynamics, rather than pulling out the pieces that contain the most variance, we would rather pull out the pieces that are the most coherent.

More formally, suppose we want to find the series

$$\zeta_i(t) = \int_0^{2\pi} A_j^*(\alpha) \exp(i\alpha t) dZ_x(\alpha)$$

and,

$$\eta_i(t) = \int_0^{2\pi} B_j^*(\alpha) \exp(i\alpha t) dZ_y(\alpha)$$

(with the standardizations

$$A_j^T(\lambda)\, A_j^*(\lambda) = 1,\ B_j^T(\lambda)\, B_j^*(\lambda) = 1$$

that have maximum coherence compared to any other such series that are independent at all frequencies to the series ζk, and ηk, with $k<j$. This problem is the standard canonical correlation problem, but now in the frequency domain. The solution to this problem (Brillinger 1981, chapter 10) is found by solving, at each frequency, the pair of eigenvalue problems:

$$f_{xx}^{-1}(\lambda)\, f_{xy}(\lambda)\, f_{yy}^{-1}(\lambda)\, f_{yx}(\lambda)\, A_j(\lambda) = \mu_j\, A_j(\lambda)$$

$$f_{yy}^{-1}(\lambda)\, f_{yx}(\lambda)\, f_{xx}^{-1}(\lambda)\, f_{xy}(\lambda)\, B_j(\lambda) = \mu_j\, A_j(\lambda)$$

The resulting series, $\zeta j(t)$ and $\eta j(t)$, are called the jth canonical series, and their coherence, $u_j(\lambda)$ is called the jth canonical coherence.

It is computationally more stable to solve:

$$f_{yy}^{-1/2}(\lambda)\, f_{yx}(\lambda)\, f_{xx}^{-1}(\lambda)\, f_{xy}(\lambda)\, f_{yy}^{-1/2}(\lambda\; V_i(\lambda) = \mu_j\, V_j(\lambda)$$

Then $B_j(\lambda)$ is proportional to $fyy^{-1/2}\, V_j(\lambda)$ and $A_j(\lambda)$ is proportional to $fxx^{-1}(\lambda)\, fxy(\lambda)\, fyy^{-1/2}(\lambda)V_j(\lambda)$. It follows from Brillinger (1981, chapter 10) that the jth canonical series has a spectral density at frequency:

$$A_j^*(\lambda)\, f_{xx}(\lambda)\, A_j(\lambda)\ [\text{resp. } B_j^*(\lambda)\, f_{yy}(\lambda)\, B_j(\lambda)]$$

and the cross-spectrum between the jth canonical series and the original series given by:

$$f_{xx}(\lambda)\, A_j(\lambda) \text{ and } f_{yy}(\lambda)\, B_j(\lambda)$$

From these relationships we can calculate the gain, coherence, and phase between the original series and each of the canonical series. The phase relationships are calculated so that the jth canonical series for each variable has phase zero in area 4. Thus the phases as presented have meaning only in terms of the same variable at a different location. For example, because in area 9 yellowfin CPUE may have a phase of 7.84 fortnights and SST a phase of –8.5 fortnights, it does not mean that SST has preceded CPUE by 16.34 fortnights. Rather, for example, if the CPUE canonical series has a phase of –8.00 with the SST canonical series, then SST would precede CPUE by only 8.3 fortnights. Thus, results from the canonical analysis must be interpreted with care.

When actually calculating the canonical analysis, we found that the matrix:

$$\begin{bmatrix} f_{xx} & f_{xy} \\ f_{yx} & f_{yy} \end{bmatrix}$$

was never of full rank (i.e. 22); in fact it usually had rank of only 10 or 11. As the analysis is based only on the submatrices of this matrix, we overcame this problem by calculating the singular value decompositions of fxx and fyy:

$$f_{xx} = Q_{ox}\, D_x\, Q_{ox}{}^*;\ f_{yy} = Q_{oy}\, D_y\, Q_{oy}{}^*;$$

where the Q's are orthogonal matrices and the D's are diagonal matrices. Then the six smallest diagonal elements of Dx and Dy were forced to zero, and the matrices fxx and fyy were reconstructed. This removed the singularity in each case by eliminating from each set of variables the six linear combinations of the area spectral density at that frequency. Usually only 5% or less of the total spectral power was removed, so that very little information was lost by this process.

The bulk of our analysis depends on spectral and other least squares techniques. These techniques generally ''smooth'' or average over different occurrences, so that the results display the ''normal'' pattern of relationships. However, for many fisheries problems, particularly in relation to the environment, the abnormal happening may be of equal interest (such as El Niño in the Pacific). Further refinements of our techniques are needed to examine this type of situation.

8666

FRAME TRAWL FOR SAMPLING PELAGIC JUVENILE FISH

RICHARD D. METHOT
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

The frame trawl is a micronekton net designed to sample pelagic larval and juvenile fish that avoid plankton nets and pass through the mesh of large midwater trawls. The mouth of the frame trawl is a rigid, square frame with an area of $5\ m^2$. The bridle attaches at two points and leaves the mouth relatively unobstructed and vertical at all tow speeds. A modified Isaacs-Kidd depressor can be attached behind the frame for midwater sampling, or floats can be attached for surface sampling. The frame trawl compares favorably with other similar-size samplers. In sea trials, juvenile anchovy and other species up to 200 mm long, and thousands of 15-20-mm anchovy larvae have been collected.

RESUMEN

La red de marco es una red para micronecton diseñada para muestrear larvas y juveniles de peces pelágicos que evitan redes de plancton y pasan a través de la malla en redes de media agua de gran tamaño. La boca de la red de marco es un marco rígido, cuadrado, con un área de $5\ m^2$. La brida se afirma en dos lugares, manteniendo la boca relativamente libre de obstrucción y en posición vertical a cualquier velocidad de arrastre. Un depresor Isaacs-Kidd modificado puede ser adicionado detrás del marco en caso de muestreo a media agua o, pueden ser agregados flotadores para muestreo superficial. La red de marco presenta ciertas ventajas con respecto a otros muestradores de tamaño similar. En muestreos experimentales, se colectaron juveniles de anchoveta y otras especies de hasta 200 mm de largo, y miles de larvas de anchoveta de 15-20 mm.

INTRODUCTION

Studies of recruitment variation in marine fishes have focused on the early larval stages. Certainly these animals have a high mortality rate, and variations in prey abundance, predators, and ocean currents probably cause substantial variation in this mortality. The capability to detect larvae in poor physiological condition is now well developed (Theilacker 1986), but this is only one step in the study of recruitment variation. Several important questions have not been addressed: How rapidly does the high larval mortality decline? Where are large, old larvae found if adverse drift is a significant factor? Most important, what is the earliest life stage at which an index of recruitment can reliably be made?

There are two aspects to this last question. The first concerns variation in mortality with respect to life stage; larval fish studies cannot provide the final answer to recruitment variation if juvenile mortality varies substantially. The second aspect concerns our ability to sample each life stage. Late larvae and juveniles effectively avoid standard plankton samplers (Murphy and Clutter 1972), leaving a gap in our knowledge until the larger juveniles become available to commercial fishing gear and large midwater trawls (Mais 1974).

The goal is development of a quantitative sampler for late larval and juvenile pelagic fish. This sampler will elucidate larval drift and migration, and extend the survivorship curve throughout the larval life stage. Surveys of late larvae will make it possible to partition recruitment variation into two components: one explainable by variation in larval mortality and the other probably caused by variation in juvenile mortality.

Ideally, a new sampler should: (1) filter a large volume in order to detect rare organisms; (2) be unobtrusive to reduce avoidance by larger organisms; (3) retain little plankton to reduce sorting costs; and (4) be easy to handle. Because the late larval and juvenile stages of some species are surface-associated, it should be possible to tow the sampler near the surface, yet away from disturbance caused by the towing vessel. Because other species inhabit deep waters, it is important to be able to open and close the net's mouth. All of these design characteristics are affected by mouth area, tow speed, mesh size, and bridle design.

The primary target for this sampler is 15-60-mm northern anchovy (*Engraulis mordax*). This size range overlaps the larvae captured by the 70-cm bongo plankton nets and the juveniles captured by 10-15-m midwater trawls. The plankton net has 0.505-mm mesh, and filters about $150\ m^3$ when sampling along an oblique trajectory from 70 m to the surface (Smith and Richardson 1977). The midwater trawl has variable mesh with a cod-end liner of about 6 mm and a mouth area of over $100\ m^2$; it filters over $100{,}000\ m^3$ in a horizontal tow (Mais 1974). The new sampler should have

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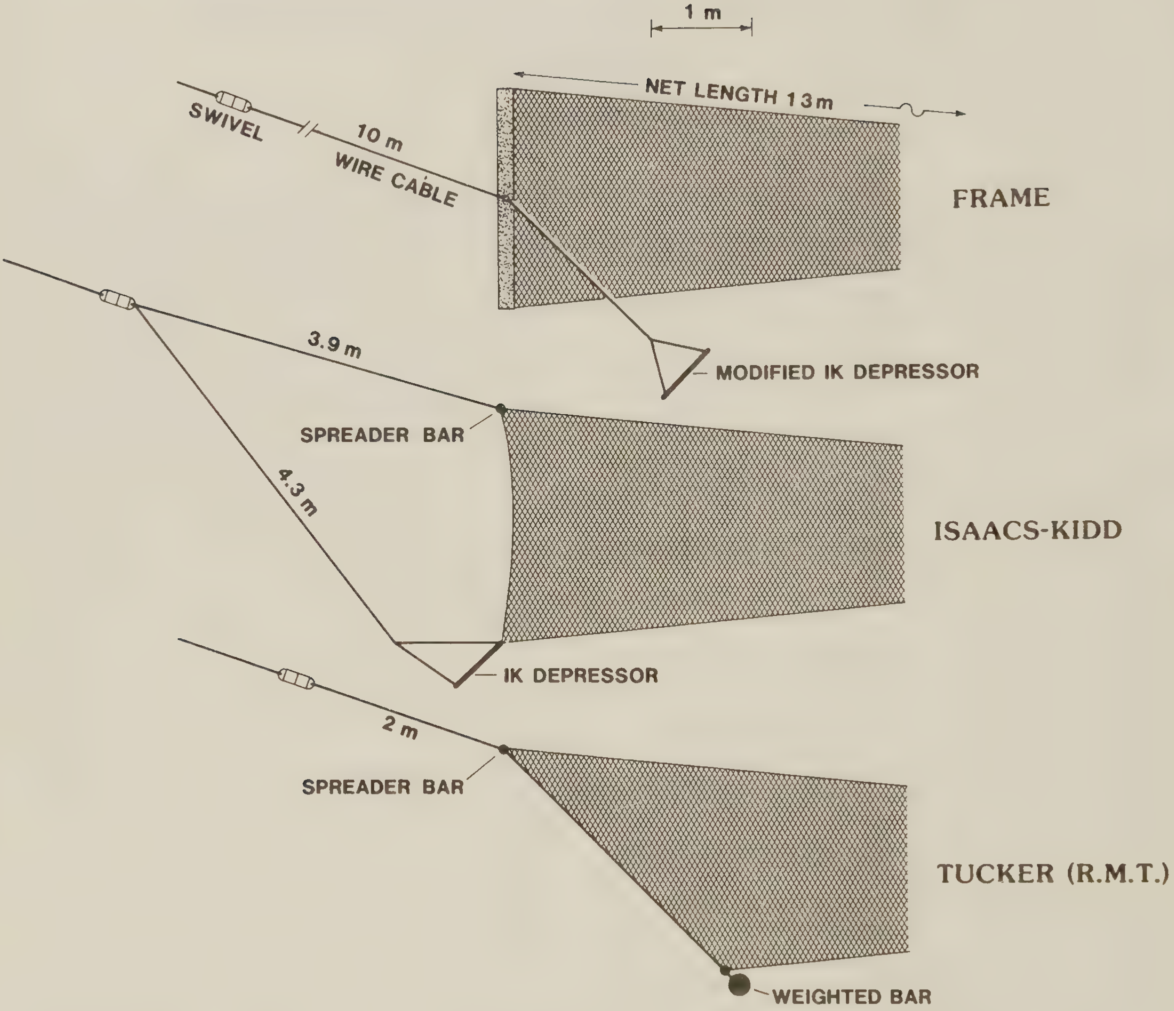

Figure 1. Profiles of Isaacs-Kidd midwater trawl, Tucker trawl (rectangular midwater trawl), and frame trawl. All are drawn with a mouth area of 5m^2.

2-mm mesh to retain most 15-mm larvae and extrude most plankton, and it should be able to easily filter 10,000 m^3 to detect less-abundant late larvae and juveniles.

This target volume can be obtained by a large, slow net or a smaller, faster net. Whether juvenile fish can avoid a large, slow net more easily than they can avoid a small, fast net is uncertain. The disturbance created by the fast net may negate any advantage of its speed. The target volume is difficult to achieve with a small, fast net because the range of reasonable speeds (0.5-3.0 m/sec) is less than the range of reasonable mouth areas (1.0-100.0 m^2). A compromise of size and speed seems reasonable, with attention to making the net as quiet and unobtrusive as possible.

Two widely used candidates for this sampler (Figure 1) are the Tucker trawl (Tucker 1951), also called rectangular midwater trawl (Baker et al. 1973), and the Isaacs-Kidd midwater trawl (Isaacs and Kidd 1953). The rectangular midwater trawl (RMT) has been built in sizes ranging from 1 m^2 to more than 25 m^2 and is usually equipped with an opening-closing mechanism for the net's mouth. A common design has a 8-m^2 mouth area, 4.5-mm mesh, and a 291-kg weight in the lower bar (Baker et al. 1973). The disadvantage of this design is that the mouth angle (and area) vary with tow speed because the bridle attaches only to the top of the net frame. This restricts the RMT's tow speed to less than about 1.0 m/sec.

The Isaacs-Kidd midwater trawl (IKMT) was de-

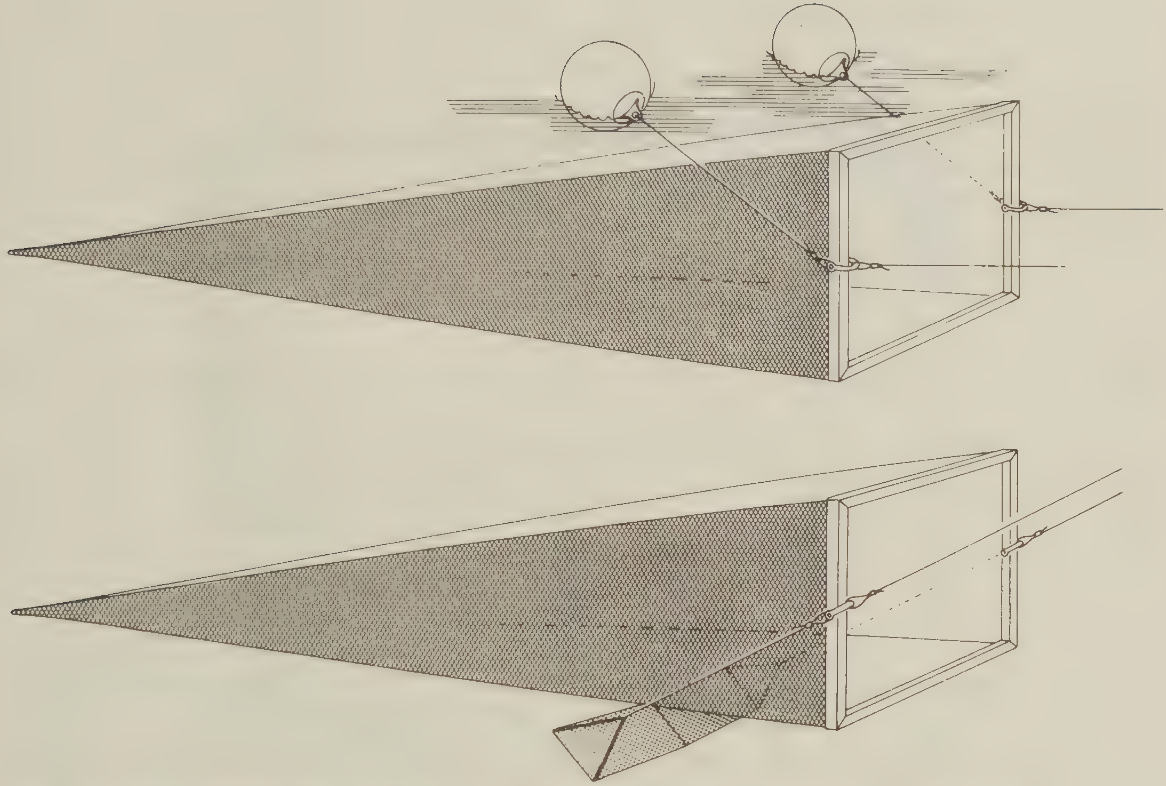

Figure 2. The frame trawl in its surface configuration with floats (*above*), and in its subsurface configuration with the Isaacs-Kidd depressor (*below*).

signed to be a fast (2.-3. m/sec), deep-diving net for sampling mesopelagic organisms. A common size has a depressor width of 3 m and a mouth area of about 7-8 m^2. The disadvantage of the IKMT is that the depressor is located at the leading edge of the lower portion of the net, where it and its bridle must create substantial disturbance and increase avoidance by larger fish. In addition, neither the RMT nor the IKMT are effective near-surface samplers: they must either be towed very near the vessel or use unreasonably large floats.

A fixed-frame trawl with integral depressor was developed by Matuda et al. (1978) for sampling Antarctic krill. Their goal was the same as mine: to improve on the tow speed and mouth angle limitations of the RMT, and on the lower-bridle disturbance of the IKMT. The 2.5 × 2.5-m sampler they designed has only an upper bridle and maintains a nearly vertical mouth opening and constant ratio of depth to wire over a wide range of tow speeds. This design succeeds in moving the bridle away from the net's opening, but the upper and lower depressor built into the frame must substantially disturb the flow of water near the net's mouth. Matuda et al. (1978) note inflated flowmeter readings that probably resulted from the lower bridle's deflecting water toward the net's mouth.

DESCRIPTION OF FRAME TRAWL

The frame trawl described here (Figures 1 and 2) is a medium-size net (Pearcy 1983) that shares some characteristics of the bongo, the RMT, and the IKMT. The mouth of the net is surrounded by a rigid square frame, and the long bridle attaches only to the midpoints of two opposite sides. These features give the frame trawl a vertical mouth at all tow speeds, and its mouth is nearly free of obstruction by the bridle (Figure 3). Bridle extensions can be attached to a modified Isaacs-Kidd depressor or to floats, so the frame trawl can quickly be converted from a midwater trawl to a surface trawl. The frame trawl described here has 2-mm mesh, a mouth area of 5 m^2, and a routine tow speed of 2.0 m/sec. It is designed primarily for quantitative oblique tows in the upper 100 m of the water column and cannot be opened or closed during a tow.

The frame is constructed of heavy (schedule 80) steel pipe with an inside diameter of 3.2 cm (1.25-inch) welded to a 10-cm (4-inch)-wide strip of 0.64-cm

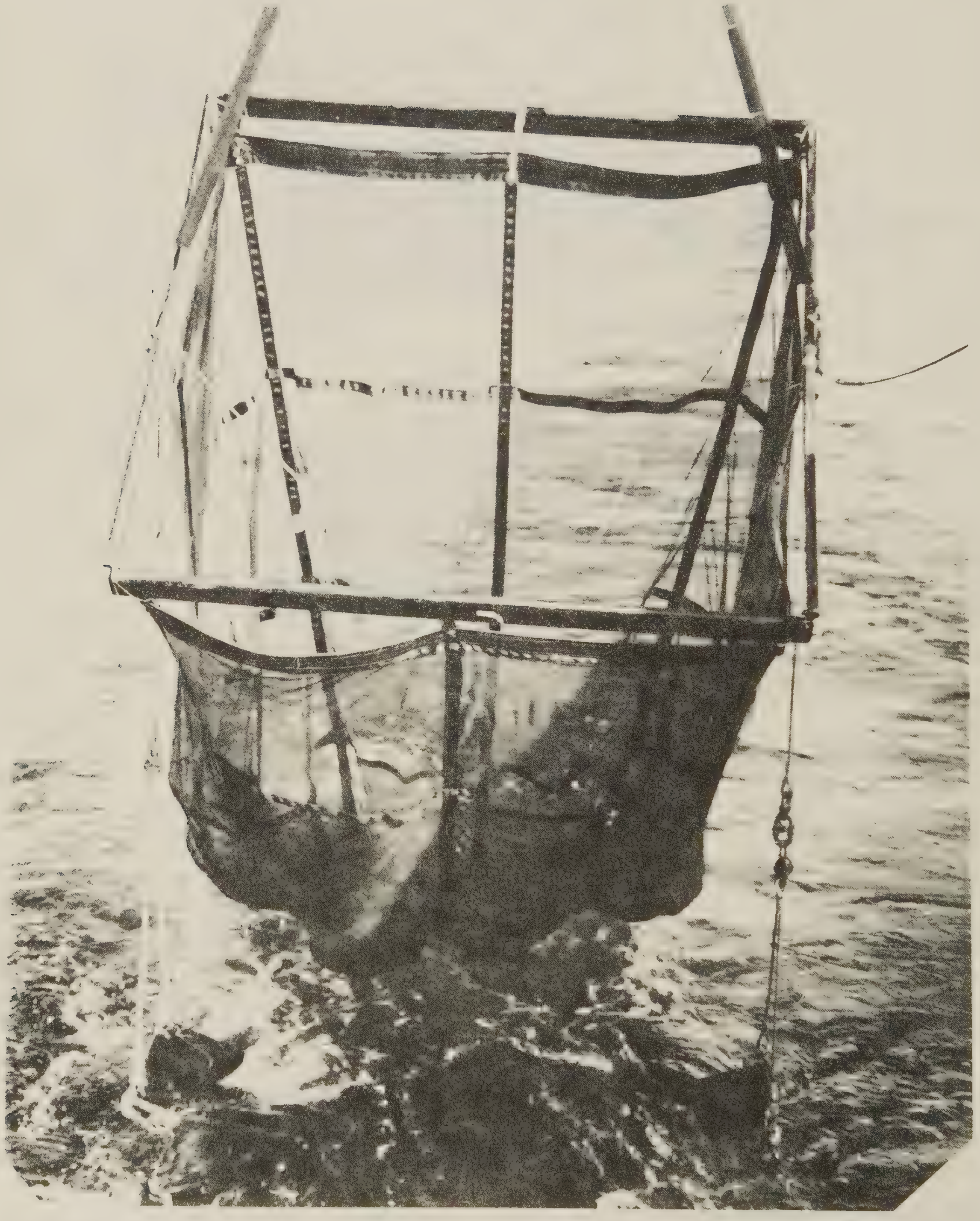

Figure 3. Photograph of the frame trawl being deployed. The depressor hangs below the net frame at this time, then trails farther aft during the tow. The two sides of the bridle are held together by the block (pulley) and separate farther when more tow cable is let out. Rigid clip-on cable fairings are on the lower portion of the bridle to reduce cable vibration. A flowmeter is in the lower left corner of the frame

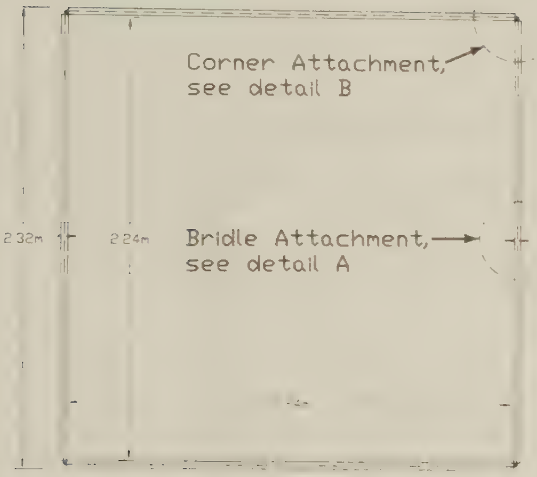

Figure 4. Dimensions of the frame trawl with 5 m² mouth area. See Figure 5 for construction details

(0.25-inch) plate steel (Figure 4). U-shaped bridle attachments made of 1.3-cm (0.5-inch) steel rod are welded to a reinforced section of the midpoint of each side (Figure 5). A corner bracket of 0.95-cm (0.375-inch) steel is welded to each end of the top and bottom and bolted to the two sides. The total mass of the frame in air is 106 kg; this could probably be safely reduced by narrowing the plate steel to about 7.5 cm.

The depressor is a dihedral, as designed by Isaacs and Kidd (Figure 6). Its dimensions are 2.44 m × 0.61 m (8 ft × 2 ft). The depressor used in the frame trawl differs from the original Isaacs-Kidd depressor in the bridle attachment. The original design had an asymmetric triangle attached by hinges to each end of the depressor. The bridle was attached to the forward-directed apex of the triangles, and the net was attached to the trailing edge of the depressor. The triangular arms were shaped so that the depressor would maintain an angle of attack (45°) that maximized the downward force.

The frame trawl has nothing attached to the trailing edge of the IK depressor; therefore the shape of the triangular arms must be modified to maintain the 45° angle of attack. Trials with a small model in a laboratory flume indicated that an isoceles triangle is a suitable shape, but the angle of attack of this modified IK depressor varies with tow speed. At zero speed, or when the depressor is very heavy, it will hang straight down with no angle of attack and generate no downward force other than its weight. At very high speed or when it has negligible weight, the depressor swings farther back and up until it is vertical (90° angle of attack) and generates maximum drag but no downward component to this drag. The mass of the depressor (65 kg in air) gives it an intermediate angle of attack. At a speed of 2.0 m/sec the 5-m^2 frame trawl dives deeper if a 35-kg (75-lb) weight is added to the depressor; the scope (ratio of wire out to net depth) was about 3.0 with the weight attached and 4.0 without the weight. The added weight brings the depressor's angle closer to the 45° optimum. A steep wire angle (low scope) is desirable because it moves the bridle farther out of the mouth opening (Figure 2).

The two floats are heavy-duty vinyl fishing floats. Each has a volume of 200 liters.

The bridle is constructed of 11-mm (7/16-inch) cable. The main bridle consists of two 10-m sections (Figure 7). At one end they come together at a swivel, which is connected to the towing cable. The opposite ends of the main bridle sections terminate at swivels attached to the U-shaped brackets inside the frame. These swivels at the brackets may be unnecessary if torque-balanced cable is used for the bridle. Attached to the U-shaped brackets on the trailing edge of the frame are 1.5-m sections of cable that terminate with quick-release connectors. These connectors can be attached either to the modified IK depressor or to the floats. The total mass of the bridles is 32 kg.

The net is constructed of knotless black nylon 1/8-inch stretch mesh (2 mm × 3 mm oval pores) and black nylon webbing (5-cm width, seat belt strap material). There are eight longitudinal straps and nine circumferential straps (ribs). The mesh material is sandwiched between two layers of strap material, and the entire sandwich is sewn through with zigzag stitching. The net is attached to the frame by extending the eight longitudinal straps about 50 cm beyond the mouth of the net (Figure 8). Heavy, 10-mm (3/8-inch) grommets are set in these strap extensions and in the mouth rib. The straps are looped around the frame, and the grommets in the strap are bolted to the grommets in the mouth rib. The mesh has low porosity, about 23%, and the length of the net is 10 m, so the ratio of pore area to mouth area is low (1.6) when allowance is made for the substantial area occluded by straps. Increasing the net length to 13 m and reducing the number of ribs to two (plus the rib around net mouth) would increase the ratio of pore area to mouth area to about 2.6.

The terminal end of the net is attached to a section of 20-cm-diameter plastic pipe. A cod end constructed of 0.505-mm mesh is attached to the terminal end of the pipe with a band clamp.

The net of 2-mm mesh sandwiched between 5-cm-wide nylon straps has proved difficult to repair. Rips in the net often require replacing sections of the straps, and it is difficult to achieve sufficient strength in longitudinal strap junctions that are resewn.

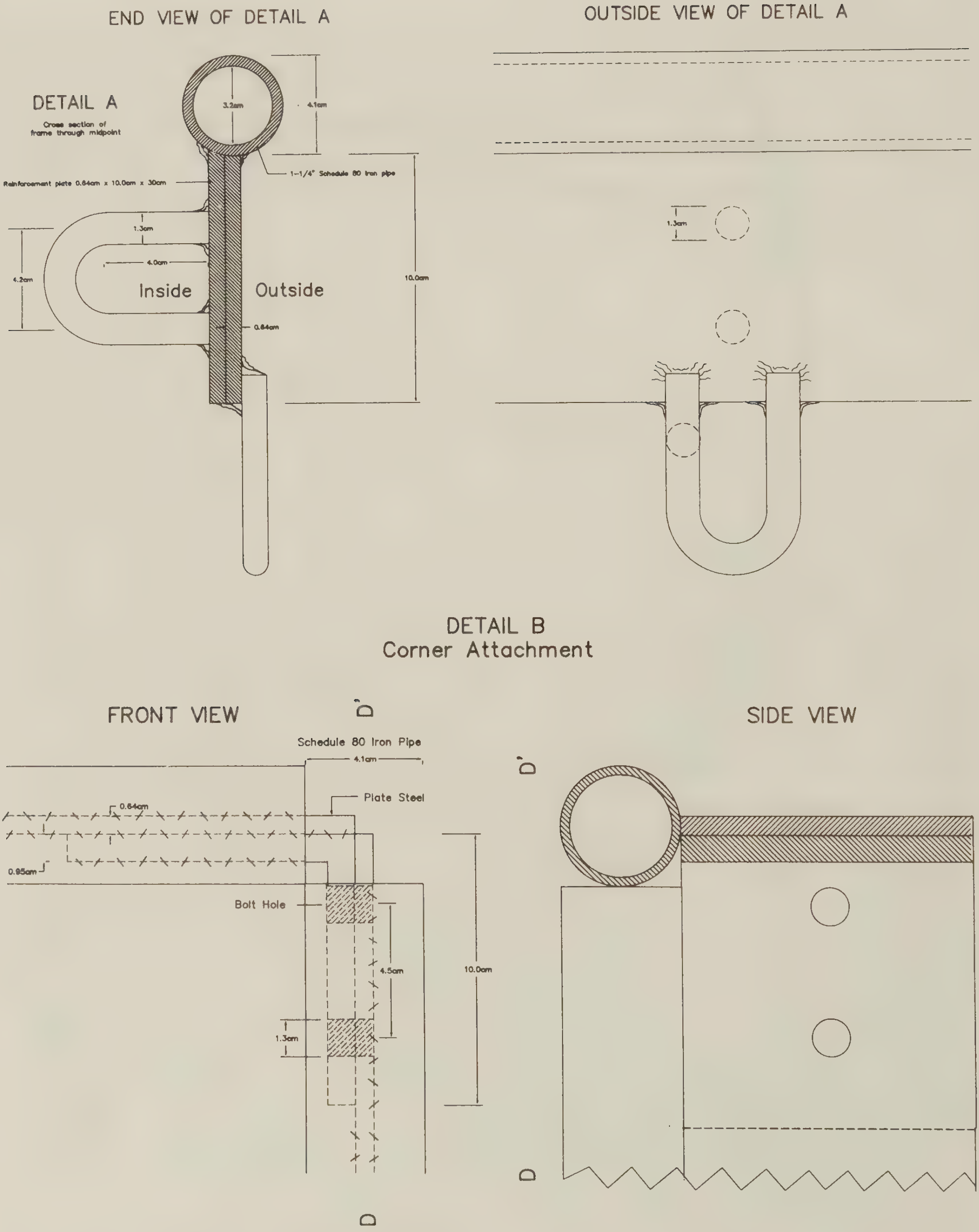
END VIEW OF DETAIL A
OUTSIDE VIEW OF DETAIL A
DETAIL A
Cross section of frame through midpoint
3.2cm
4.1cm
1-1/4" Schedule 80 Iron pipe
Reinforcement plate 0.64cm x 10.0cm x 30cm
1.3cm
4.0cm
4.2cm
Inside
Outside
10.0cm
0.64cm
1.3cm
DETAIL B
Corner Attachment
FRONT VIEW
SIDE VIEW
D'
D'
Schedule 80 Iron Pipe
4.1cm
Plate Steel
0.64cm
0.95cm
Bolt Hole
4.5cm
10.0cm
1.3cm
D
D

Figure 5. Construction details of the frame trawl: *detail A*, bridle attachment; *detail B*, corner attachment.

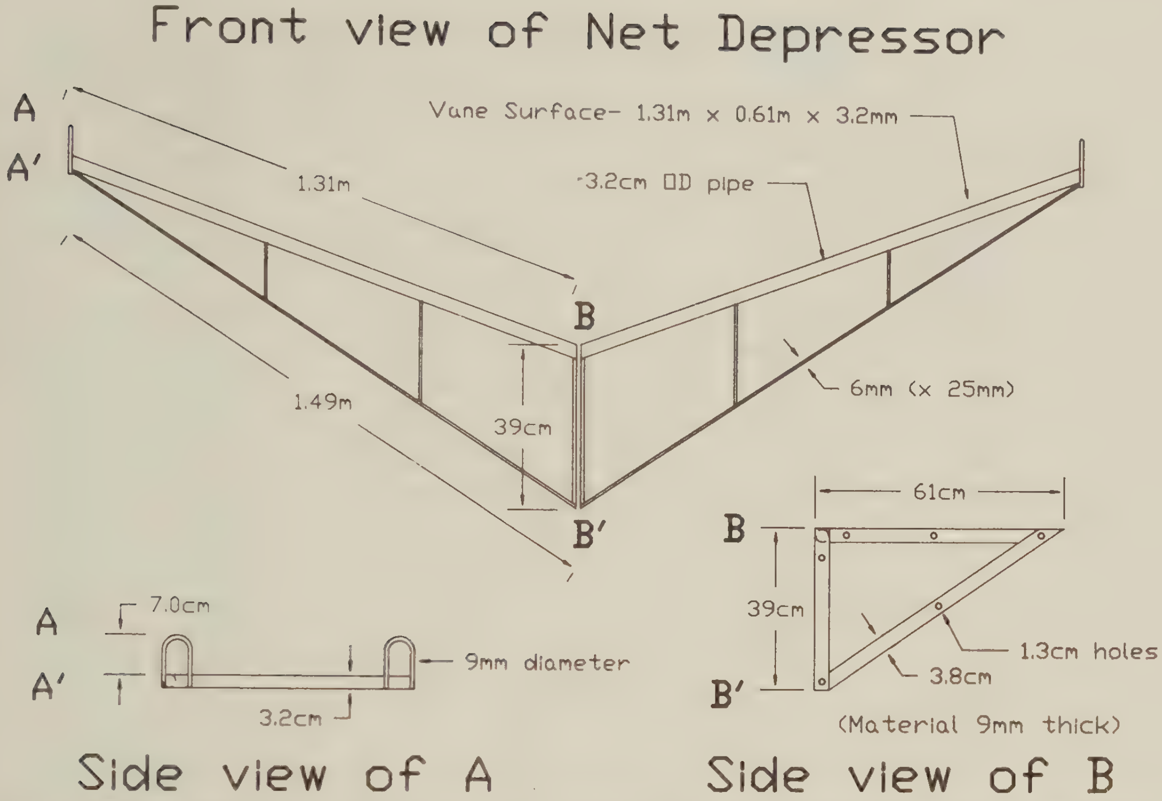

Figure 6. Modified Isaacs-Kidd depressor used with the frame trawl. The hinged asymmetric triangle on the Isaacs-Kidd depressor has been replaced with two U-shaped brackets. The two halves of the frame bolt together with bolt holes shown in side view of B.

As an alternative, we constructed a second, 13-m-long trawl net with 6.4-cm (2.5-inch) stretch mesh and four longitudinal strain members of 16-mm (5/8-inch) rope. An eye was spliced into the forward end of the strain members for attachment to the frame. A liner of 2-mm mesh was installed inside the trawl. IKMT nets built in this manner have proved durable. This alternative net performed well in a brief sea trial, but was significantly heavier than the original design.

SEA TRIALS

The frame trawl has been to sea three times: January, March, and July 1985. For the first two trials we used a prototype version with a rectangular mouth opening ($1.73 \text{ m} \times 1.45 \text{ m} = 2.5 \text{ m}^2$). This frame size was selected to roughly fit the net from a 6-ft IKMT. For the July trial we used the 5-m^2 working version of the frame trawl.

The January trial was designed to test the basic net principle. We made 16 tows to determine the relation between ship's engine RPM, net speed, and net depth. The frame trawl proved to be easy to handle and to have stable tow trajectories. The deployment procedure is as follows:

1. The tow cable is passed through a block at the top of a stern A-frame.
2. The A-frame is tilted forward to lift the block to its highest position.
3. The swivel and forward portion of the bridle are pulled through the block until the frame and depressor are lifted from the deck.
4. The net is tossed into the water.
5. The tow cable is slowly paid out while the A-frame is tilted aft.
6. After the frame is in water and the swivel clears the block, the tow cable can be rapidly paid out.

The March 29-31 trial was the first test of the frame trawl as a sampler. Eighteen tows were made between San Diego, California, and Santa Catalina Island and along the NE shore of the island. All tows were made at night at a speed of 2 m/sec. Four of the tows were made with floats rather than the depressor. Oblique tows to sample the upper 50 m of the water column were made with 200 m of wire out and retrieved at a rate of 10 m/

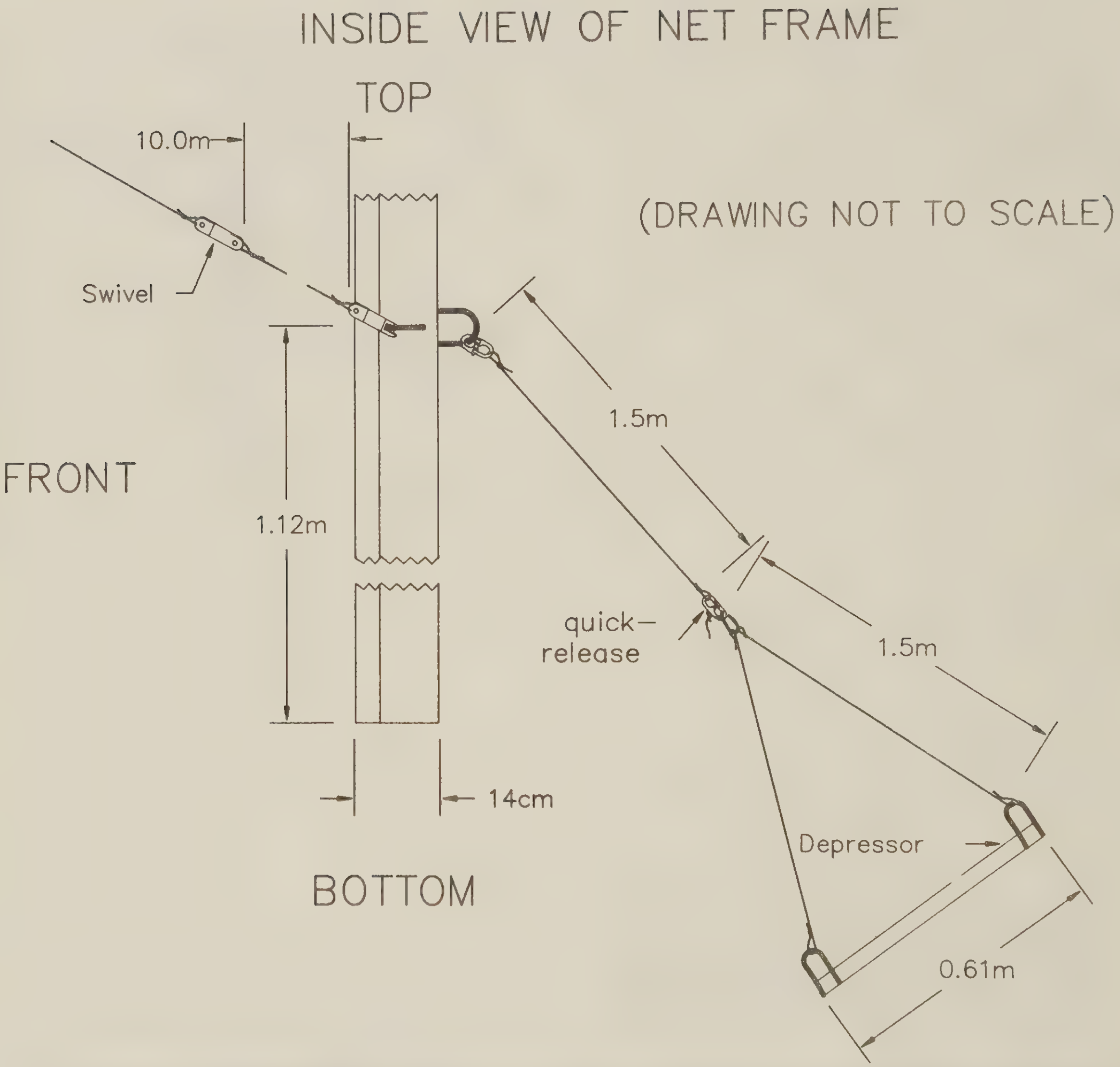

Figure 7. Bridle lengths for the frame trawl. The swivel and anterior portion of the main bridle are designed to be drawn through the block to lift the frame off the deck. The quick-release connectors can be attached either to the depressor or to the floats.

min. Surface tows were made with 100 m of wire out and a duration of 20 min. During surface tows the ship made a slow turn to keep the net to the side of the wake. A flowmeter installed in the mouth of the net indicated that tow speed ranged from 1.88 to 2.36 m/sec (mean = 2.00) and that the volume filtered during the oblique tows ranged from 5,600 to 7,900 m^3 (mean = 7,150).

Large anchovy larvae were consistently collected (Table 1). Most larvae shorter than 10 mm probably were extruded through the 2-mm mesh. The extrusion of small larvae may be reduced if the net is lengthened. This will increase the ratio of pore area to mouth area and decrease the velocity of water through the pores. The high catches of larvae larger than 15 mm are very encouraging; this size range is poorly sampled by plankton nets because of avoidance and low volume filtered.

Catch rates of all size categories were greater in oblique tows than in surface tows among tows 3-9 (Table 1). In the 15-20-mm size range the mean catch was 0.6 larvae per 1,000 m^3 in surface tows and 11.3 per 1,000 m^3 in oblique tows. No larvae larger than 20 mm were

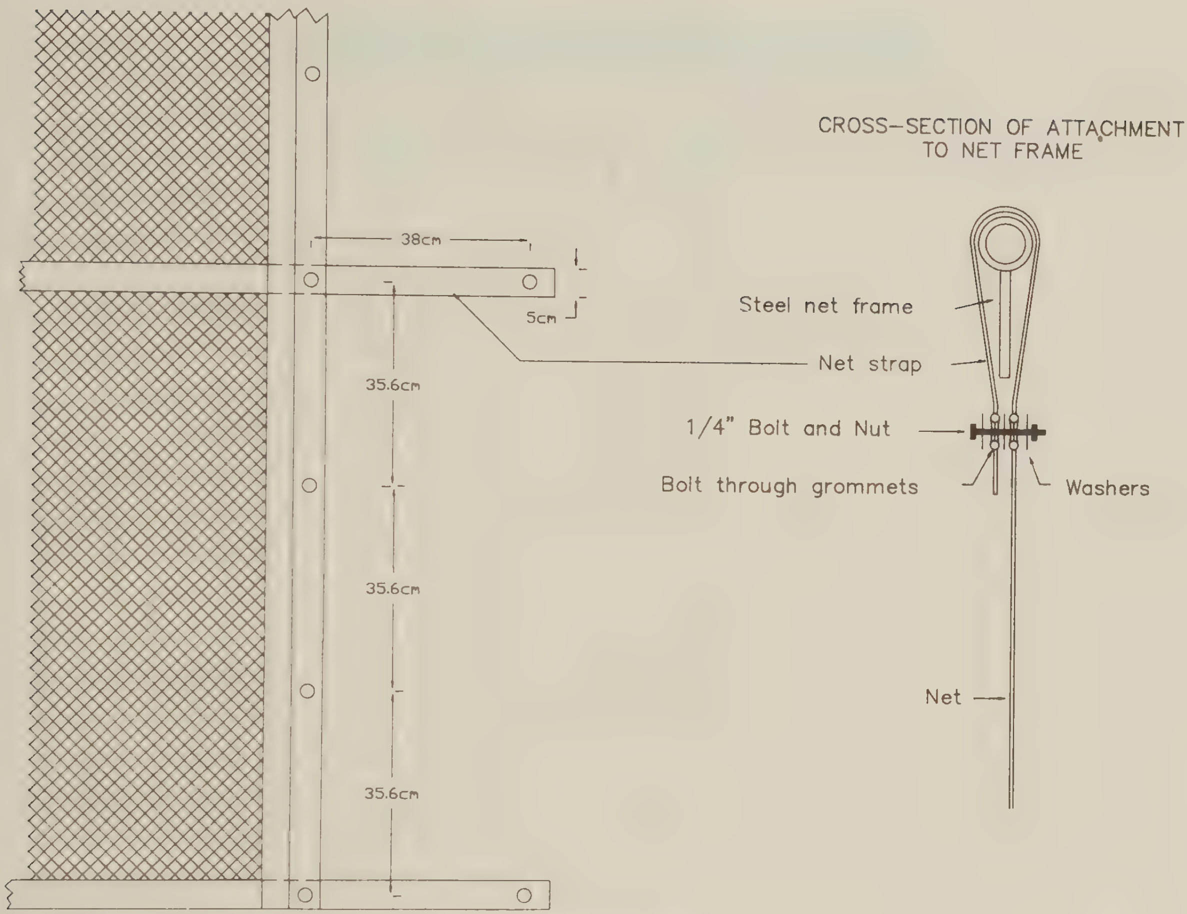

Figure 8. Profile of the anterior portion of the net showing straps used for attachment to the frame.

collected in surface tows. The difference between surface and oblique tows is greater in terms of abundance per unit sea-surface area rather than density. Multiplying the oblique results by 50 m (the maximum depth sampled) and the surface results by 1.45 m (the height of the frame, which is the maximum depth sampled) indicates that abundance of 15-20 mm larvae is 565 per 1,000 m^2 in the upper 50 m, and only 0.87 per 1,000 m^2 in the upper 1.45 m.

Juveniles and adults of other species were commonly collected in excellent physical condition (Table 2). The capture of two *Merluccius* was especially encouraging. The frame trawl was designed to be an effective sampler of age-0 fish, but the *Merluccius* were age 1+.

The 5-m^2 frame trawl was tested on the night of July 29-30, 1985. Ten tows were conducted along the coast north of San Diego. Tows 5 and 6 were over bottom depths of 100 m, and tows 7-15 were over bottom depths of 55-66 m. Surface tows were alternated with oblique tows, and tow procedures duplicated those in the March test of the prototype. Large anchovy larvae were commonly collected (Table 3), and sardine larvae often constituted about 10% of the clupeiform larvae (Table 4). Catch rates of anchovy in surface tows were similar to catch rates in oblique tows (Table 3). Larvae shorter than 10 mm had greater density in surface tows, and larvae longer than 10 mm had greater density in the oblique tows. Only two anchovy larvae longer than 20 mm were collected in surface tows.

DISCUSSION

The average abundance of anchovy larvae collected by the frame trawl is similar to historical catches by the bongo plankton net. Hewitt and Brewer (1983) analyzed bongo collections from the nearshore (<43-m bottom depth) between San Diego and Point Conception. From January to June 1980, the catch of 10-15-

TABLE 1
Catches of Anchovy Larvae in Prototype Frame Trawl, March 1985

Tow number and type	Number of larvae	Abundance per 1,000 m^3					Longest larva (mm)	Location
		<10 mm	10-15 mm	15-20 mm	>20 mm	Total		
1 O	117	4.7	9.3	1.2	0.1	15.3	23.0	San Diego to Santa Catalina
3 O	523	9.3	41.7	15.9	0.0	66.1	19.0	San Diego to Santa Catalina
4 S	63	0.9	7.2	0.0	0.0	8.1	14.0	San Diego to Santa Catalina
5 O	751	33.1	58.1	8.0	2.0	100.2	21.0	San Diego to Santa Catalina
6 S	54	2.0	4.1	0.4	0.0	6.5	18.0	San Diego to Santa Catalina
7 O	432	6.8	49.9	10.9	1.4	68.4	27.0	San Diego to Santa Catalina
8 S	65	2.0	4.5	1.4	0.0	8.0	16.5	San Diego to Santa Catalina
9 O	278	7.5	18.3	10.4	5.4	41.6	23.5	San Diego to Santa Catalina
10 H	87	4.6	4.0	0.8	0.6	10.0	25.0	San Diego to Santa Catalina
11 O	498	12.4	64.7	11.5	0.0	88.6	19.0	3 km offshore N
12 O	1,242	39.1	117.2	6.5	0.0	162.7	17.5	3 km offshore S
13 O	827	31.9	60.3	9.1	1.1	113.8	21.0	2 km offshore N
14 O	1,622	78.0	117.0	8.2	2.1	205.2	22.5	2 km offshore S
15 O	370	17.3	27.6	1.9	0.0	46.8	16.0	1 km offshore N
16 O	353	22.2	22.2	1.9	0.0	46.3	17.0	1 km offshore S
17 O	557	17.9	40.2	27.7	3.6	89.4	24.0	toward San Diego
18 O	744	43.0	48.1	8.2	3.1	102.4	22.0	toward San Diego
Mean for tows 3-9:								
S		1.6	5.3	0.6	0.0			
O		14.2	42.0	11.3	2.2			

O = oblique, S = surface, H = horizontal. Tow 2 was discarded because of the large volume of gelatinous zooplankton. Tows 11-16 were made parallel to the island's shoreline.

mm anchovy larvae averaged 13.8 larvae per tow, and average abundance was 6.7 larvae per m^2 of sea surface. Hewitt and Methot (1982) estimated that the average abundance of 10-15-mm larvae throughout the larval habitat in March 1978 was 8.9 larvae per m^2. In March 1985 the prototype frame trawl collected an average of about 400 10-15-mm larvae per tow, or 2.6 per m^2, and these numbers must be inflated to account for the unmeasured extrusion through the 2-mm mesh. In July 1985 the four nighttime, oblique frame trawl tows

TABLE 2
Fish Other Than Anchovy Collected by Prototype Frame Trawl, March 1985

Tow number and type	Number of larvae	Larger specimens
1 O	57	(2) bathylagidae 87, 90 mm; several myctophidae
3 O	271	(2) bathylagidae 75, 77 mm; many myctophidae
4 S	7	—
5 O	212	(5) bathylagidae 90-105 mm
6 S	15	—
7 O	47	(1) *Porichthys* 120 mm
8 S	13	—
9 O	6	—
10 H	9	—
11 O	105	—
12 O	121	(1) *Merluccius* 160 mm
13 O	174	—
14 O	178	(1) *Merluccius* 170 mm
15 O	52	(1) *Porichthys* 120 mm
16 O	23	(1) *Porichthys* 120 mm; (1) pleuronectidae 31 mm
17 O	123	(6) bathylagidae 37-82 mm; several myctophidae
18 O	111	(4) bathylagidae 87-101 mm; several myctophidae

O = oblique, S = surface, H = horizontal.

TABLE 3
Catches of Anchovy Larvae in the Frame Trawl, July 1985

Tow number and type		Number of larvae	Abundance per 1,000 m³					Longest larva (mm)
			<10 mm	10-15 mm	15-20 mm	>20 mm	Total	
5	O	9,142	68.2	443.5	170.6	0.0	682.2	17.5
6	S	3,336	42.4	163.9	76.3	0.0	282.7	18.0
7	O	510	6.0	30.7	17.5	0.5	54.8	24.0
9	S	1,956*	67.2	74.7	7.5	0.0	149.3	19.0
10	O	1,462*	18.1	67.3	42.7	1.3	129.4	20.0
11	S	2,311*	81.9	75.4	6.6	0.0	163.9	17.5
12	O	1,699*	7.0	29.5	75.8	28.1	140.4	25.0
13	S	801*	26.4	18.6	3.9	0.0	48.8	18.0
14	O	159	4.0	8.4	3.5	0.2	16.1	21.0
15	S	99	0.7	3.8	2.9	0.2	7.4	20.5
Mean for tows 5-13:								
	S		54.5	83.2	23.6	0.0		
	O		24.8	142.8	76.7	7.5		

*Includes some sardine larvae. O = oblique, S = surface.
Tow 5 began at 32°59.2′N, 117°19.6′W, 100-m bottom depth. Subsequent tows proceeded northward along the coast; tows 7-15 were over bottom depths of 55-66 m. Tow 15 began at 33°14.0′N, 117°29.2′W. Tows 14 and 15 were taken during daylight (0550 and 0719 PDT).

collected an average of 1,600 10-15-mm larvae per tow; average abundance was 7.1 larvae per m^2 (uncorrected for extrusion through the 2-mm mesh). Although the bongo net and frame trawl indicate similar abundances of 10-15-mm anchovy larvae, the frame trawl estimates will be greater when corrected for extrusion, and the frame trawl will be able to detect and quantify much lower larval abundances because it filters over 100 times as much water per tow.

Variance of catch per tow seems lower with the frame trawl than with smaller plankton samplers. Hewitt and Methot (1982) estimate that the coefficient of variation (standard deviation / mean) is about 1.6 for 10-mm larvae collected with the bongo plankton net and 3.5 for 14-mm larvae. The CV for catch of 10-mm larvae by the prototype frame trawl was only 0.6, and the CV was 0.75 for 15-mm larvae. The similarity of catch between replicate frame trawl tows was especially high (Table 1; tow numbers 11-12, 13-14, and 15-16). This low variance must be due to the large volume filtered (about 7,000 m^3) and long distance towed (about 3 km), which integrates much small-scale patchiness.

The frame trawl seems to be a successful and adaptable design. It can be deployed alone, with depressor, or with floats. The model used here had a mouth area of 5 m^2, and frames ranging from 1 to 10 m^2 seem feasible. The frame trawl is superior to the bongo plankton net for sampling large anchovy larvae. Further sea trials will be necessary to determine the overlap in sampling effectiveness between the frame trawl and large midwater trawls.

ACKNOWLEDGMENTS

I am thankful for the suggestions and support provided by Bill Flerx, Reuben Lasker, Paul Smith,

TABLE 4
Fish Other Than Anchovy Collected by Frame Trawl, July 1985

Tow number and type		Number of sardines	Number of others	Larger specimens
5	O	0	139	(1) *Merluccius* 49 mm
6	S	121	16	(2) pipefish 94, 173 mm
7	O	17	20	(3) goby 28-37 mm; (2) *Sebastes* 22-27 mm; sardine 15-17 mm
9	S	220	63	(1) scienidae 140 mm
10	O	present	46	(29) goby 26-43 mm; (1) *Porichthys* 31 mm; (3) pleuronectidae 22-30 mm
11	S	70	61	—
12	O	?	49	(3) goby 22-39 mm; (1) *Sebastes* 22 mm; (7) *Porichthys* 2-27 mm; (3) *Porichthys* 155-185 mm; (8) pleuronectidae 23-28 mm
13	S	?	28	—
14	O	1	4	sardine 17.5 mm
15	S	3	4	sardine 15.0-21.0 mm

O = oblique, S = surface, (   ) number of specimens.

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8667

Management of Dungeness Crab Fisheries

R. D. Methot Jr.

National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, USA

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Management of Dungeness crab fisheries in the states of California, Oregon, and Washington was reviewed by the Pacific Fishery Management Council in 1979 and may be considered in three categories: conservation of the resource, maintenance of product quality, and reduction of conflicts. Size limits and prohibition of landing female crabs are the primary conservation measures. Additionally, escape ports in the crab traps reduce wastage. Season closures maintain product quality by reducing the harvest of recently molted crabs. Area closures reduce conflict between commercial and recreational fishermen.

Current management measures seem sufficient to prevent biological overexploitation but may not be optimal. Size limits reduce the necessity for a prohibition on harvest of females. Size limit levels may be too large when enforcement, optimum yield and genetic selection issues are considered. Consideration of the optimal level of effort in the crab fishery is complicated by the multispecies nature of the west coast's fishing fleet. High crab abundance during the late 1970s resulted in an increase in the size of the crab fleet and a large fraction of legal-sized male crabs are now harvested in the first few weeks of the season. Efforts to deal with this apparent overcapacity must consider the great mobility of vessels between the crab, salmon, albacore, shrimp, and groundfish fisheries

En 1979, le Pacific Fishery Management Council a évalué la gestion de la pêche aux crabes dormeurs dans les États de la Californie, de l'Oregon et de Washington. Celle-ci peut être divisée en trois catégories, soit la conservation des ressources, le maintien de la qualité du produit et la limitation des conflits. Les principales mesures de conservation sont l'imposition de limites de taille et l'interdiction de débarquer des crabes femelles. De plus, des ouvertures spéciales pratiquées dans des casiers à crabes permettent de réduire les pertes. L'imposition de périodes saisonnières de fermeture permet de maintenir la qualité des produits en réduisant la récolte des crabes qui viennent de muer. L'interdiction de la pêche dans certaines zones aide à réduire les conflits entre pêcheurs commerciaux et sportifs

Les mesures de gestion pratiquées à l'heure actuelle semblent suffisantes pour empêcher la surexploitation biologique mais ne sont pas nécessairement optimales. Les limites de taille réduisent la nécessité de l'interdiction de la récolte des femelles. Les limites de taille imposées pourraient toutefois être trop grandes en regard de la mise en application des règlements, du rendement optimal et de la sélection génétique. La question du niveau d'effort optimal pour la pêche des crabes est compliquée par le grand nombre d'espèces pêchées par les flottes de la côte Ouest. L'abondance de crabes durant la fin des années 1970 a entraîné un accroissement des flottes de caseyeurs et une grande partie des crabes mâles de taille réglementaire sont maintenant capturés durant les premières semaines de la saison de pêche. Afin de régler la question de cette surcapacité apparente, il faut se pencher sur la question de la grande mobilité des navires entre les lieux de pêche aux crabes, aux saumons, aux germons, aux crevettes et aux poissons de fonds

Introduction

There are two striking characteristics of Dungeness crab fisheries on the United States' west coast: the fishery in central California (San Francisco area) collapsed in about 1960 to 10% of previous sustained landings and has not recovered, and the fishery in northern California (Eureka area) has oscillated with a period of about 10 yr and an amplitude of more than a factor of 10. Fisheries in Oregon and Washington also have oscillated but with lesser amplitude. Studies of stock dynamics in California (Peterson 1973; Botsford and Wickham 1974, 1978; McKelvey et al. 1980; Wild and Tasto 1983) have not conclusively demonstrated whether these fluctuations are environmentally driven or due to density-dependent mechanisms (Botsford 1986). Regulations intended to conserve the stock were first enacted by the State of California in 1897–1905 and have been modified little since then. These regulations have a biological basis (Miller 1976) but have not been quantitatively scrutinized for their effect on stock dynamics. The Pacific Fishery Management Council (1979), which manages fisheries in the U.S. Fishery Conservation Zone along the coasts of California, Oregon, and Washington, examined the status of crab fisheries and considered options for improved management, but no action was taken. This paper explores justification for current regulations and describes characteristics of the fishery with regard to current interest in control of the level of effort in this and other west coast fisheries.

Fishery History

A recent review of Dungeness crab fisheries in California (Dahlstrom and Wild 1983) identifies commercial landings at San Francisco in 1863 and a substantial fishery using hoop nets by the 1880s. Landings increased from 882 metric tons (t) in 1889 to 1662 t in 1899 then peaked at 2318 t in 1904. During this period there were indications of declining catch rates in the immediate vicinity of San Francisco and area of the fishery expanded. In response to concerns for conservation of the resource, possession and sale of female crabs was prohibited in 1897, a 2-mo closed season was enacted in 1903 and a minimum size limit became law in 1905. These regulations were insufficient to reverse the stock's decline. Landings from 1905 through 1913, although undocumented, apparently declined. When landing statistics became available again in 1915, landings had declined to about 100 t.

Dungeness crab catch at San Francisco remained low (200-900 t) through the 1923-24 season. In 1925-26 landings increased to the level observed in the 1890s but did not attain 2300 t again until 1948-49. Landings ranged from 1000 to 4000 t during 1949-60 (Fig. 1) then collapsed and have not recovered. Current landings, about 600 t, are similar to those of the early 1920s.

Much effort has been directed towards determining the cause of the collapse of central California's Dungeness crab stock in the early 1960s (Wickham 1979; Wild and Tasto 1983). However, the decline in landings during 1905-13 suggests that the 1960s' collapse was not an unique event. Wild et al. (1983) suggests that persistence of warm water and anomalous northward transport after the 1957-58 El Niño caused poor recruitment in central California. This correlation is logical because Dungeness crab in central California are near the southern limit of the species' range. It is possible that earlier changes in abundance of this stock also were due to climatic shifts. Unfortunately, consistent and continuous measurements of marine environmental conditions do not extend prior to the 1920s. Douglas (1980) used tree ring data to infer high air and sea temperatures in southern California during the mid-1800s and Hubbs (1948) noted extreme northward range extensions of many subtropical species during 1853-60. The Dungeness crab fishery which developed in central California during the late 1800s may have been possible because cooler environmental conditions (Douglas 1980) occurred then. Figure 10 in Douglas (1980) indicates warmer water occurred again during the early 1900s. These sparse and indirect data suggest that climatic conditions may play a role in determining abundance of Dungeness crab along the coast of central California.

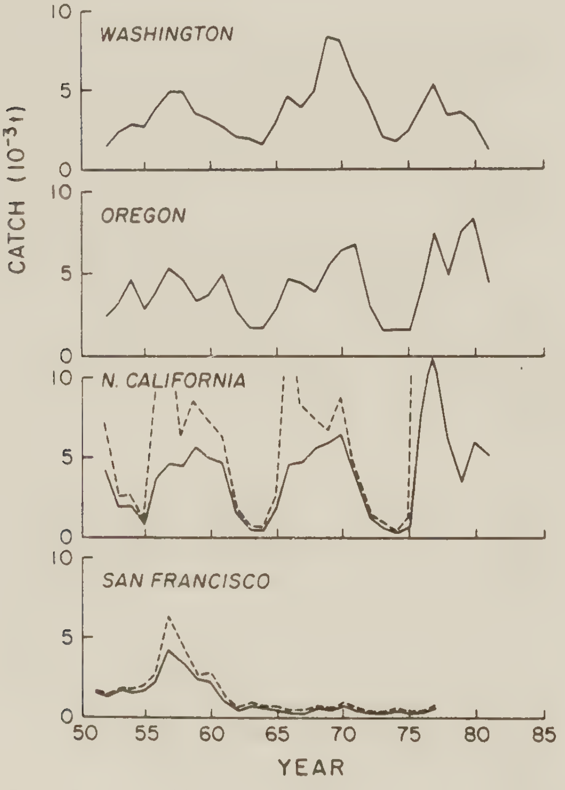

FIG. 1. Commercial landings of Dungeness crabs in California, Oregon, and Washington. Dashed line indicates pre-season abundance estimated form CPUE on cumulative catch (Methot and Botsford 1982). In northern California CPUE remained high throughout three seasons: 1956-57, 1965-66, and 1976-77, so pre-season abundance in these years must have been much greater than the catch.

A major Dungeness crab fishery did not start in northern California until the late 1930s. Expansion of this fishery began after 1941 when the canning prohibition and ban on export of Dungeness crab from several northern California counties were repealed. In the 1945-46 season the northern California catch first exceeded the central California catch. Since then northern California landings have oscillated between high catch periods of about 6 yr duration followed by low catch periods of about 4 yr (Fig. 1). Amplitude of the cycle has been increasing and the stock in 1984 seems near the end of the fourth high catch period which began in 1975-76. Landings off Oregon and Washington also exhibit a cyclic nature, but with lesser amplitude.

Development of Regulations

Management considerations in Dungeness crab fisheries include conservation of the resource, maintenance of product quality, and reduction in user conflicts Regulations designed to achieve these goals now control size and sex of crab which can be landed, type of fishing gear, fishing areas and fishing seasons.

Concern over decline in stock abundance first became an issue in the San Francisco area during the 1890s. Possession and sale of female Dungeness crab by commercial fishermen was prohibited in 1897 to protect the resource from overfishing. This regulation remains in effect today in California, Oregon, and Washington. Only California's recreational fishermen may take female Dungeness crab

Prohibition on female harvest preceded the size limit by 8 yr, but establishment of the size limit weakened the rationale for protecting females. Botsford (1984) concludes that the asymptotic mean size for females is 152 mm carapace width (excluding lateral spines) so few females are larger than the size limit. Females mature at about age 2 (90 mm) (Butler 1961) so they are mature for about 3 yr before approaching the legal size of 159 mm. Thus a size limit applied to males and females would have about the same effect as the current male size limit and female prohibition. Harvesting the few female crabs larger than 159 mm would increase yield little and may cause problems for industry because of claims (Pacific Fisheries Management Council 1979) that meat yields from female Dungeness crab are lower and that sexes would have to be separated before processing if females were landed.

The size limit for male crabs was established to protect crabs until they were mature, but there is no documented scientific analysis which determined the optimal size limit. In 1905 the limit was set at a carapace width of 152 mm (6 inches, including lateral spines). It is likely that processors' preference for large crabs was a factor in determining the level of this limit. The minimum was increased to 178 mm (7 in) in 1911 and the method of measurement was redefined slightly in 1915. In 1965 the measurement was redefined to 159 mm (6.25 in) excluding lateral spines without significantly changing the actual legal size of crab landed.

The size limit is an important constraint on the fishery. A large fraction of legal-sized male crabs are captured each year (Gotshall 1978a). Methot and Botsford (1982) examined decline in catch rate within each crab season and concluded that over 90% of legal-size male crabs were harvested in central California during each season from 1951 to 1955 and that exploitation rates greater than 80% were typical until 1964. In northern California, exploitation rate is commonly over 70%. Without the size limit a large number of smaller males also would be harvested and the possibility of overexploitation would be increased.

The appropriate size limit can be based on size at sexual maturity, yield per recruit, and enforcement problems if many crabs are near the size limit. Male crabs begin to mature at 108 mm and all males >122 mm sampled in California are sexually mature (Poole 1967) and are about 2 yr post-metamorphosis (Collier 1983). This size is 2 molts below the size limit of 159 mm (Table 1), so males have about 2 breeding seasons before entering the fishery. Size at maturity seems similar to that in the north (Collier 1983) but growth rate (molt frequency) is slower so northern males may have 3 breeding seasons before entering the fishery. Recruitment overfishing probably is not occurring and would not occur if the size limit was decreased.

The proximity of the male crab size limit to expected size at age 4 (Table 1) suggests that genetic selection for slow-growing individuals may occur. Larger age 4 males are available to the fishery and high exploitation rates (Methot and Botsford 1982) indicate that large, available males are unlikely to survive to the following mating season. Slow growing males will be below the size limit at age 4 so are likely to survive and mate for one more year. Genetic selection on male Dungeness crab could be reduced by lowering the size limit to about 150 mm so most age 4 male crabs would be available to the fishery.

TABLE 1. Growth of male crabs at three locations along the west coast. Data are from Collier (1983) who included the earlier work of Butler (1961). Tabulated values are calculated carapace widths of males after the indicated molt (instar) Ages (yr) are from Botsford (1984). Age 1 occurs in November after hatching the previous winter

Instar number	Age (yr)	Central California	Washington	Queen Charlotte Island
10		72.7 mm	68.0	72.7
11	2	90.0	84.6	90.2
108 mm — males begin to mature				
12		111.2	105.9	111.5
122 mm — all males are mature				
13	3	136.5	129.2	137.1
159 mm — males are available to the fishery				
14	4	163.0	154.9	164.5
15	5	190.9		193.7
16		220.3		224.9

Yield per recruit cannot be calculated for male Dungeness crab because growth and natural mortality data are not sufficiently precise. Growth of crabs older than about 4 yr is based primarily on molt growth increment data and does not take into account the fraction of older crabs that do not molt annually. The estimated size at age in Table 1 and size-weight relation in Botsford and Wickham (1978) indicate that weight at age of male crabs that molt annually increases by 71% from age 3 to 4 and by 57% from age 4 to 5. If natural mortality is about 0.50 (61% survival) then mortality would approximately balance growth for 3-5 yr-old male crabs, but natural mortality is not precisely known. An early estimate of 0.15 per year (Jow 1965) is remarkably low for an animal that seems to reach maximum size by age 6-7. Gotshall (1978) estimated natural mortality to be in the range 0.54 to 1.78, and the Pacific Fisheries Management Council (1979) considered values in the range 0.15-0.45. Given this imprecision, yield per recruit cannot guide establishment of the optimal size limit, but the data suggests that extreme growth overfishing is not occurring.

Setting the size limit at a local minimum in the size distribution lessens enforcement problems by reducing incidence of crabs trapped near the size limit. Such an enforcement issue was considered in establishment of the size limit for Pacific bonito (Collins et al. 1980). On this basis the current size limit of 159 mm probably is too close to expected size at age 4 (Table 1). A limit of 150 mm is more nearly equidistant between expected size at ages 3 and 4 and could reduce enforcement problems associated with the size limit. Variation in growth (Botsford 1984) will make size modes less distinct and reduce the value of considering enforcement in setting the level of the size limit.

Other regulations assist in resource conservation Some northern California bays and estuaries were closed to commercial crab fishing in 1933 and 1941. This regulation reduces conflict with recreational crab fishermen common in northern California bays and estuaries. In addition, prohibition of commercial crab fishing in northern California bays and estuaries, which have a high ratio of sublegal to legal size crabs, may reduce mortality of sublegal crabs associated with being captured and released. In central California, San Francisco and San Pablo bays are closed to commercial and recreational fishing to protect sublegal crabs.

Closed seasons conserve the resource by reducing harvest of soft-shelled (recently molted) crabs. If landed, these crabs would be a poor product and, if thrown overboard, they likely have higher mortality than hard crabs. The months of September and October were first closed in 1903. Currently season opening dates are: central California, second Tuesday in November; northern California, December 1; Oregon, December 1; and Washington, January 1 (but usually opens Dec. 1 by emergency regulation). Staggered opening dates are reasonable with regard to the north–south gradient in the date at which a high percentage of male crabs are hard (Pacific Fisheries Management Council 1979), but non-uniform opening dates cause enforcement problems. Closing dates now are in midsummer and vary somewhat among the states. Typically little fishing effort occurs during summer (Methot and Botsford 1982; Botsford et al. 1983) so the closing date has little effect on the fishery. Since 1981 California has experimented with season extensions through about August but little crab fishing effort occurred during the extensions.

Nearly the entire commercial crab harvest is taken in traps. In Washington and Oregon only traps and ring nets are legal gear. Gear restrictions are not specified in California but trawl vessels may have no more than 227 kg (500 lb) of Dungeness crab per landing. All three states require two escape ports in crab traps. These must be 108 mm (4.25 in) in diameter and be located in the upper half of the trap. Studies in Washington and Oregon (Pacific Fisheries Management Council 1979) indicate that this size retains nearly all legal-size crabs and releases many sublegals and females. Results of the Dungeness crab Research Program in California (Wild and Tasto 1983) indicate that an increase to 111 mm (4.375 in) would release about 50% more sublegal males and females with little increase in escapement of legal males. A change in the size limit to a local minimum in the size distribution should increase the effectiveness of escape ports.

About 10% of crab traps are lost each year. It is suspected that these traps continue to attract and capture Dungeness crab. California has a regulation requiring destruct devices on traps but implementation awaits development of a suitable device. The Dungeness crab Research Program (Wild and Tasto 1983) supported implementation of this regulation.

Commercial bottom trawling has been considered to be a source of mortality for Dungeness crab. Reilly (1983) monitored crab mortality aboard a commercial trawler in the San Francisco area. Overall mortality of crabs brought on deck was about 2% but soft-shelled male crabs had 20.2% mortality. The soft-shelled crabs often were crushed by the weight of the load of fish. Reilly (1983) lists several reasons why his observations probably underestimate crab mortality during normal fishing operations. Additionally, his study only addresses mortality of crabs retained by the net. Small crabs may be severely damaged as they pass through trawl mesh and recently molted crabs could be crushed by heavy trawl gear passing over them. California's Dungeness crab Research Program recommendation was to "Eliminate commercial trawl fishing in critical areas of the Gulf of Farallones during periods of peak molting (July–September) for male Dungeness crabs" (Wild and Tasto 1983). Fortunately, two factors reduce the likelihood of major crab mortality caused by bottom trawling. Trawlers cannot fish within 5.5 km (3 miles) of shore in California and they tend to fish in deeper water. Because Dungeness crab tend to occur in shallow water (Gotshall 1978b), much crab habitat is not vulnerable to bottom trawlers. Additionally, trawlers avoid crab areas because of the hazard presented to their nets by crab traps (Reilly 1983).

A second category of management measures concerns maintenance of product quality. Canning, pickling, or preserving crabs was illegal in the early years of the fishery and export of crabs from three northern California counties was prohibited (Dahlstrom and Wild 1983). The rationale for these regulations is uncertain but may be related to public health considerations because crab meat is highly perishable. Both of these regulations were repealed in 1941 and growth of the northern California Dungeness crab fishery began. The only current regulation affecting product quality is the closed season. Without this regulation a larger number of recently molted crabs, which have low meat yields, would be landed. Landing of softshelled crabs is prohibited in Washington.

The third category of management measures concerns reduction of conflict. Gear conflicts between crabbers and trawlers, salmon trollers and salmon gillnetters seems only a minor problem (Pacific Fisheries Management Council 1979). The crab fishery operates closer to shore than most trawl fisheries. In California trawling is prohibited nearshore in most areas and crab fishing extends into deep water only during the beginning of the season. The crab and salmon fisheries are separated in time. Little crab fishing occurs after opening of the salmon season in April or May.

Conflict, or at least competition, may occur between commercial and recreational crab fishermen. Regulations to reduce conflict between users include area closures and gear limitations. In Washington some areas of Puget Sound are closed to commercial crab fishing and the entire sound has a limit of 100 traps or ring nets per boat. In Oregon use of traps is prohibited in five major bays. In California major bays and estuaries are closed to commercial Dungeness crab fishing and this area closure extends 1.85 km (1 mile) into the open ocean at two northern California locations. These regulations tend to separate commercial and recreational fishing areas and greatly reduce the commercial fishing activity in juvenile crab nursery areas.

Current Fishery

Dungeness crab is one of the most valuable fisheries on the U.S. west coast. During 1980–83 the value of crab landings in northern California (Table 2) was exceeded only by the groundfish complex (flatfish, rockfish, cod, sablefish). Landings of shrimp during 1980–83 are down from their historical high during the late 1970s and salmon and albacore landings fluctuated by

TABLE 2. Value of landings ($\$US\ 10^{-3}$) in central (San Francisco area) and northern (Eureka area) California in recent years. Data are preliminary and are subject to modification (California Dep. of Fish and Game).

	1980		1981		1982		1983		Mean	
	N.CA	C.CA	N.CA	C.CA	N.CA	C.CA	N.CA	C.CA	N.CA	C.CA
Crab	9127	590	6902	475	6606	638	6926	994	7390	674
Salmon	6861	4632	7590	5549	9150	7247	1966	1115	6392	4636
Albacore	1212	1107	4189	4212	625	358	731	1732	1689	1852
Groundfish	9342	3367	9873	4393	11742	6186	9216	4900	10044	4707
Shrimp	1318	1	1512	8	2058	3	147	0	1259	3
Herring	156	16416	56	4570	61	9647	45	12437	80	10768
Other	952	863	567	395	1018	1483	335	1028	718	942
Total	28968	26976	30689	19602	31260	25562	19366	22206	27571	23587

about a factor of 5 (Table 2). On a 10-yr time scale the value of Dungeness crab landings also has oscillated about 5-fold, even though changes in price tend to buffer the value of landings from fluctuations in catch (Botsford et al. 1983). During the 1968–69 and 1969–70 seasons the average value in California was $3,940,000 ($3.94 M), during the 1971–72 and 1972–73 seasons the average value was $1.17 M and during the 1979–80 through 1982–83 seasons the average value was $8.06 M (Table 2). The Dungeness crab fishery appears sufficiently valuable to warrant attention of fishery managers.

Evidence presented earlier suggests that current regulations are sufficient to prevent overexploitation of the stock. Recruitment overfishing seems unlikely with the prohibition on female landings and the size limit on males; growth overfishing probably is not occurring but yield per recruit cannot be estimated with available data. Changes in management should not be expected to improve the magnitude of the harvest. The low level of the central California stock and the large amplitude oscillations of the northern stocks currently must be treated as conditions which fishermen and managers react to, but do not control.

A major problem in the west coast's Dungeness crab fisheries is the large capacity of the fleet. West coast fishermen tend not to specialize so any attempt to redistribute excess crab fishing effort requires knowledge of the Dungeness crab fishing fleet in relation to other west coast fisheries. The following section will describe the characteristics and mobility of the crab fishing fleet, then the problem of excess fishing effort will be reexamined.

Dungeness crab tends to be fished by small, multipurpose vessels. Crab vessels usually are converted salmon trollers or bottom trawlers (Frey 1971) and may shift to other fisheries during the off-season for crab and during poor crab fishing years. In a 1968 survey, the mean lengths of crab vessels were 11 m in central California and 12 m in northern California (Dahlstrom and Wild 1983). The Pacific Fishery Information Network, PACFIN, database (Huppert et al. 1984) provides an opportunity for examination of the crab fleet composition during 1981.

In 1981, 1439 vessels landed Dungeness crab. Vessels were categorized into high and low income groups based on total exvessel value of all species, into principal species groups based on the species which contributed the greatest fraction of the vessel's total value and into regions based on the port at which the vessel landed the greatest value. Low income vessels (< $10,000 exvessel value) were small, about 9 m, and landed only 6.3% of the Dungeness crab in 1981. High income vessels with Dungeness crab as their principal species composed 31% of the crab fleet (Table 3) and landed 66% of the crab (Table 4). These vessels averaged 11.7 m in length. High income vessels with a species other than crab as their principal species landed the second highest fraction of crab, 28%, and composed 33% of the crab fleet. These vessels were slightly larger, 12.8 m, than the principal crab vessels. Much of the crab catch by high income, principally non-crab vessels was by 15–30 m vessels fishing in Oregon and northern California (Table 4). These larger multispecies vessels seem to be the major change in composition of the crab fleet between 1968 and 1981.

In 1981, 51% of high income vessels which landed crab obtained more income from another species. Fishermen may shift to different fisheries within and between years. Within year shifting is facilitated by the limited duration of several fisheries. Crab, salmon, shrimp, and herring fishing are limited by seasonal closures and albacore fishing is limited by seasonal migration pattern (Table 5). The timing of these seasons is sufficiently staggered so that a fisherman can fish during the peak of the crab, salmon and albacore seasons or the crab and shrimp seasons. The importance of within season switching in 1981 can be considered with the PACFIN database (Huppert et al 1984). The high income vessels which landed crab comprised only 6% of the fleet but landed substantial fractions of other species groups (Table 6): herring, 8%; groundfish, 12%; salmon, 13%; albacore, 19%; and shrimp, 37%. The high value for shrimp may be due to depressed shrimp landings since the late 1970s. This latter factor may have reduced the number of vessels which target on shrimp so those vessels which fish crab and shrimp land a large fraction of the total shrimp. This argument suggests that between year shifting out of the shrimp fishery has influenced the analysis within 1981. In years with poor salmon or albacore catch (i.e. 1983, Table 2), it is likely that a higher fraction of the catch of these species is

TABLE 3. Sizes of fishing vessels in 1981. Vessels are categorized according to total exvessel value of their landings (< or > $10,000), to the state of their principal port and their principal species. Principal port is defined by the total exvessel value of landings. Principal ports in California are divided at Monterey into a south region and a north region which contains the San Francisco and Eureka areas. Principal species is determined by the exvessel value of each species landed: CRAB+ indicates that a vessel's principal species was crab, CRAB− indicates that the principal species was not crab but some crab were landed, CRAB0 indicates that no crab were landed by that vessel in 1981. Weighted mean vessel length uses the vessel's crab catch as the weighting factor. Data are from the annual vessel summary file of the 1981 PACFIN database (Huppert et al. 1984).

	Vessel length class (m)					Length (m)	
	0–9	10–15	16–21	>21	Total Number	Mean	Wt. mean
		Exvessel value < $10,000					
CRAB+							
WA	141	41	3	0	185	8.1	8.4
OR	21	40	2	4	67	11.5	11.9
N.CA	62	42	3	1	108	9.4	10.2
TOTAL	224	123	8	5	360	9.1	9.6
CRAB−							
WA	25	10	0	0	35	9.0	8.9
OR	27	19	1	0	47	9.2	9.1
N.CA	46	20	1	0	67	8.9	8.8
S.CA	1	1	0	0	2	9.8	9.8
TOTAL	99	50	2	0	151	9.0	8.9
CRAB0							
TOTAL	8494	2463	140	39	11136	8.3	—
		Exvessel value > $10,000					
CRAB+							
WA	32	63	3	0	98	10.7	12.0
OR	22	145	8	1	176	11.7	12.0
N.CA	30	129	17	1	177	12.2	13.2
TOTAL	84	337	28	2	451	11.7	12.5
CRAB−							
WA	21	45	5	0	71	11.4	12.1
OR	21	93	43	7	164	13.8	15.9
N.CA	30	168	26	6	230	12.5	15.4
S.CA	3	6	2	0	11	11.7	15.9
TOTAL	75	312	76	13	476	12.8	15.4
CRAB0							
TOTAL	669	1480	458	216	2823	14.1	—

by vessels that also fish crab. Conversely, in years with low crab abundance a large amount of effort must shift to other fisheries. Continuation of the PACFIN database for several years should provide the information necessary for separation of between and within year shifts in effort. Better definition of between and within year effort shifting is critical as schemes to control effort in these fisheries are evaluated.

The number of vessels landing Dungeness crab in northern California has fluctuated similarly to the 10-yr cycle of catch (Botsford et al. 1983). At low points in the catch cycle (1954–55, 1963–64, and 1973–74) only 95, 117, and 93 vessels respectively have fished Dungeness crab. By the end of each high catch period the number of vessels had doubled: 196 vessels in 1951–52, 213 vessels in 1960–61, and 250 vessels in 1970–71. At the onset of the current high catch period in the 1975–76 season, the number of vessels increased at an unprecedented rate (299 vessels in 1975–76) and during the calendar year 1981, 418 high income vessels and 177 low income vessels fished crab in California (Table 3).

The number of vessels in the fishery influences seasonal distribution of catch (Table 7). The fraction of the season's catch landed in December through February has fluctuated between 50% and 90% during the 1960s–early 1970s (Methot and Botsford 1982). Higher values tend to occur at the end of the high catch periods as the number of vessels increases and at the beginning of the low catch periods as the vessels' exit from the fishery lags behind the decline in abundance (Botsford et al. 1983). Catch during the final months of the season tended to parallel the total season catch. This indi-

TABLE 4. Total crab landings (t) by vessels in 4 length categories. The vessels also are categorized according to total value of landings, the state of their principal port and whether their principal species was crab. See Table 3 for definition of categories. Data are from the annual summary file of the PACFIN database (Huppert et al. 1984)

	Landings (t)				
	Vessel length class (m)				
	0–9	10–15	16–21	> 21	Total
	Exvessel value < $10,000				
CRAB +					
WA	204.7	76.1	4.1	—	284.9
OR	28.8	71.0	4.7	7.1	111.7
N.CA	65.4	59.9	9.7	1.0	136.0
TOTAL					532.5
CRAB −					
WA	14.5	4.6	—	—	19.1
OR	11.2	8.4	0.1	—	19.8
N CA	21.6	7.9	0.3	—	29.8
S CA	0.1	0.1	—	—	0.2
TOTAL					68.9
	Exvessel value > $10,000				
CRAB +					
WA	209.1	955.7	57.3	—	1222.2
OR	169.4	1883.2	128.9	5.9	2187.3
N CA	284.1	2085.9	454.4	32.6	2857.0
TOTAL					6266.6
CRAB −					
CA	43.5	157.3	9.4	—	210.3
OR	34.7	626.1	525.3	76.0	1262.2
N CA	51.4	663.3	274.8	194.3	1183.8
S CA	1.1	1.0	43.2	—	45.2
TOTAL					2701.5

TABLE 5. Seasonal distribution of landings (t) of major species groups which have strong seasonal patterns. The seasonal patterns for these species, except albacore, are dictated by closed fishing seasons. The tabulated values are for all of California in 1981 (preliminary data obtained from California Dep. of Fish and Game).

	Landings (t)				
	Crab	Salmon	Albacore	Herring	Shrimp
JAN	657	0	0	2962	0
FEB.	244	0	9	1216	1
MAR.	79	0	<1	83	0
APR.	109	3	0	<1	375
MAY	64	767	0	<1	450
JUNE	20	287	5	<1	230
JULY	6	893	532	6	209
AUG.	7	602	3210	84	199
SEPT	<1	179	3157	0	289
OCT.	<1	<1	1648	<1	97
NOV.	54	0	259	0	1
DEC.	2477	0	7	1492	1

cates that large early season harvests, which occurred in some high catch years, were not large enough to depress the late season harvests.

During the 1980s the late season catch was low despite high total season catches (Table 7). The number of vessels in the crab fishery is at a record high and the fraction of the total season catch landed during December through February also is at record levels. The fraction landed during December alone is at a very high level: 1980–81, 86%; 1981–82, 66%, and 1982–83; 77%

The probable cause of the low late season harvests is reduction in abundance of legal-sized males caused by the large early season harvest. Historically the fishery has been able to land up to about 90% of legal males in a season (Methot and Botsford 1982). Currently they seem able to achieve this exploitation rate in the first few months of the season. Another possible cause for low late season catches is increased within year shifting of effort. As the catch rate of crab declines within the season the multi-purpose fishing vessels may be capable of making more money by shifting effort to salmon, shrimp or groundfish. Thus increased participation by multi-purpose fishing vessels may have exaggerated the within season fishery dynamics.

Packing the catch into the first few weeks of the season has several adverse consequences: competition between fishermen increases as each deploys more gear to get a share of the harvest, processors must freeze

TABLE 6. 1981 landings in California, Oregon and Washington of 6 important species groups by 6 categories of fishing vessels. CRAB+ vessels obtained most of their income in 1981 from Dungeness crab. CRAB− vessels landed some Dungeness crab but obtained most of their income in 1981 from a different species group. CRAB0 vessels did not land Dungeness crab in 1981. These data are from the annual summary file of the 1981 PACFIN database (Huppert et al. 1984)

Species group	Vessels with < $10,000			Vessels with > $10,000			TOTAL (t)
	CRAB+	CRAB−	CRAB0	CRAB+	CRAB−	CRAB0	
	Percent of landings						
Crab	5.6	0.7	0	65.5	28.2	0	9569
Salmon	0.3	0.8	25.9	4.2	8.8	60.0	17817
Albacore	<0.1	0.1	3.3	5.0	13.7	77.9	12973
Groundfish	<0.1	<0.1	1.1	1.0	11.1	86.7	113691
Shrimp	<0.1	<0.1	0.2	4.2	32.4	63.2	18139
Herring	<0.1	0.3	6.2	0.9	7.1	85.5	7013
	Percent of vessels						*N* vessels
	2.3	1.0	72.3	2.9	3.1	18.3	15405

TABLE 7. Trends in catch and effort in the northern California (Eureka area) Dungeness crab fishery (Methot and Botsford 1982; Botsford et al. 1983). Data for the seasons 1980–81 through 1982–83 are preliminary figures from the California Dep. of Fish and Game

Season	Total catch (t)	Percent in Dec.–Feb.	Catch in May–Aug. (t)	*N* Vessels
1960–61	4555	75	382	213
1961–62	1475	90	70	190
1962–63	409	82	29	124
1963–64	370	66	39	117
1964–65	1805	72	89	164
1965–66	4528	53	332	169
1966–67	4672	73	271	168
1967–68	5508	86	186	173
1968–69	5828	85	337	194
1969–70	6397	81	318	237
1970–71	3555	42[a]	476	250
1971–72	1153	88	87	190
1972–73	523	80	59	153
1973–74	160	46	26	93
1980–81	4691	99	31	—
1981–82	3672	94	50	595[b]
1982–83	1915	90	22	—

[a] Low harvest in January, probably price dispute between fishermen and processors

[b] Number of crab vessels in calendar year 1981 from PACFIN database (Huppert et al. 1984)

more crab for longer periods, and distributors have only a brief supply of fresh crab. The foreshortened season may be the major problem with the Dungeness crab fishery (Meyer Resources Inc. 1983), but effort management schemes which would distribute the catch more evenly over the season will be difficult to evaluate and implement. The great decline in crab catch per effort within in each season (Methot and Botsford 1982) and the seasonal availability of opportunities to shift into other fisheries are two obvious complicating factors.

Excess capacity in the Dungeness crab fleet also may indicate a situation of economic overfishing. Total harvest seems to be divided among too many fishermen so the average profit per fisherman is less than it could be. Schemes for reducing effort in the crab fishery were considered by the Dungeness Crab Project of the State/Federal Fisheries Management Program (Collinsworth and Silverthorne 1976). The Project attempted to determine optimum level of effort (number of traps) for the coastwide fishery and considered three means of regulating effort at an appropriate level: licensing vessels and/or traps, taxes on landings, and quotas for individual fishermen. The Project did not explicitly consider the multispecies aspect of this fishery. The propensity of fishermen to shift effort between fisheries confounds economic analysis of effort limitation in any one of the fisheries. The concentration of crab fishing effort into the early part of the season may not be the optimal scheme for harvesting the crab resource, but fishing heavily on crab then shifting to other species may be the optimal multispecies fishery. An additional complication, if a license or individual quota scheme is to be implemented, is determining current fishery participants. This determination is hindered by the between and within year shifting of effort between fisheries. Not all potential crab fishermen will fish crab every year.

Interviews with fishermen indicate that crab fishermen do not feel that a major problem exists in the crab fishery (Meyer Resources Inc. 1983). The overcapacity problem is greater in the salmon fishery and recent poor shrimp abundance has created overcapacity in that fishery. The problem in the crab fishery is the shift of vessels from these other fisheries into the crab fleet.

The anticipated decline in crab landings over the next few years will have repercussions outside of the crab fishery. The great capacity of the current crab fleet probably will not hinder a recovery of the stock; the female prohibition and male size limit seem more than adequate to protect the reproductive potential of the stock. However, while the stock is at the low level, fewer vessels will be able to fish crab profitably. Vessels which currently are not able to operate profitably in the salmon or shrimp fisheries will not have the option of supplementing their income by fishing crab during the winter. As vessels leave the crab fleet during the mid 1980s, there seem few opportunities for them in other species. If the Pacific Fisheries Management Council is to consider management of the effort in the salmon and groundfish fleets, they must simultaneously consider the Dungeness crab fishery.

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OXYGEN SENSITIVE AFFERENT INFORMATION ARISING FROM THE FIRST GILL ARCH OF YELLOWFIN TUNA

WILLIAM K. MILSOM and RICHARD W. BRILL

Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, Hawaii, 96813, U.S.A.

Abstract. Single nerve fiber discharge was recorded from O_2 sensitive receptors in the first gill arch of the yellowfin tuna, *Thunnus albacares*, *in vitro*. These receptors were innervated by the vagus nerve and increased their discharge in response to decreasing perfusion rate, decreasing perfusion P_{O_2} and, in most fibers, to decreasing external P_{O_2}. Fibers responding to environmental hypoxia exhibited an exponential increase in discharge to decreasing external P_{O_2} with a sensitivity similar to that exhibited by cat carotid body chemoreceptors. Indirect evidence suggests that these receptors are located near the gill vasculature and are more sensitive to changes in arterial P_{O_2} than water P_{O_2}. Their response characteristics and hypoxic sensitivity strongly implicate them as the afferent limb in the cardiac responses and perhaps also the ventilatory responses exhibited by tuna to environmental hypoxia.

Chemoreceptors
Teleost fish
Vagus nerve
Heart rate
Thunnus albacares

Environmental hypoxia has been shown to elicit both respiratory and cardiovascular responses, of varying magnitude, in all fish that have been studied to date. Whereas the ventilatory response in teleost fish is strong, consisting of increases in both respiratory frequency and tidal volume, very little response is shown by elasmobranch fish (see Shelton *et al.*, 1986, for review). Although there is some evidence to implicate the pseudobranch of teleost fish as a possible receptor site involved in the ventilatory response (Laurent, 1967, 1969; Laurent and Rouzeau, 1969, 1972; Barets *et al.*, 1970) most data implicates putative arterial chemoreceptors, possibly located within the central nervous system (Satchell, 1961; Davis, 1971; Dejours, 1973; Bamford, 1974; Holeton, 1977).

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* Correspondence to: W.K. Milsom, Department of Zoology, University of British Columbia, Vancouver, B.C., Canada, V6T 2A9.

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The cardiac response to environmental hypoxia, in both elasmobranchs and teleosts, consists of an immediate, intense bradycardia accompanied by an increase in cardiac stroke volume (Randall and Shelton, 1963, Piiper *et al.*, 1970; Butler and Taylor, 1971). Often, in teleosts, these changes are evenly matched and thus produce little change in cardiac output (Holeton and Randall, 1967; Marvin and Heath, 1968). In elasmobranchs, the receptors involved in producing this response are diffusely spread throughout the orobranchial and parabranchial cavities and are innervated by cranial nerves V, VII, IX and X (Butler *et al.*, 1977). In teleosts, they are primarily confined to the first gill arch and innervated by cranial nerves IX and X (Smith and Jones, 1978; Daxboeck and Holeton, 1978; Smith and Davie, 1984).

Although the general location and innervation of the receptors involved in these cardiac responses have been described in elasmobranchs and teleosts, nothing is known of their exact location or response characteristics. The arteries supplying the first two branchial arches in these fishes are homologous with the carotid and aortic arches of higher vertebrates and it has been suggested that the phylogenetic fate of the O_2 sensitive receptors located in the branchial arches and gills, and innervated by the IXth and Xth cranial nerves in fishes may be in the discrete carotid and aortic bodies of terrestrial vertebrates (Butler *et al.*, 1977). If this were the case, the O_2 receptors located in fish gills might be expected to exhibit similar properties to those of the carotid and aortic bodies. To date, there have been no recordings made from O_2 sensitive receptors in the primary gill arches of any fish. In the present study, we have recorded afferent impulses from the Xth cranial nerve innervating the 1st arch of the yellowfin tuna, *in vitro*, in an attempt to locate O_2 sensitive chemoreceptors and, if present, to characterize their responses to hypoxia.

Materials and methods

Recordings were made from 15 yellowfin tuna, *Thunnus albacares*, (1–2 kg body weight) obtained from local fishermen and maintained in outdoor holding tanks at the Kewalo Research Facility. Animals were supplied with well aerated, running sea water (25 ± 1 °C) and fed a diet of smelt, krill and squid. For experiments, animals were netted from the holding tank, given an intracardiac injection of 4000 IU Heparine and killed by a sharp blow to the head followed by pithing. The afferent artery to the first gill arch on one side was immediately cannulated (P.E. 90 tubing) and perfused with aerated tuna saline (1.17% NaCl, pH 7.35, P_{CO_2} 12 mm Hg) containing 20 IU/ml Heparin and filtered with a 0.2 μm filter. All other vessels supplying the gill were severed but not ligated. The Xth cranial nerve (vagus) was isolated at the nodose ganglion and, along with the entire gill arch, was dissected free and suspended in a 25 °C bath of aerated tuna saline (fig. 1). The pressure head on the perfusion line was adjusted to 120 cm H_2O, slightly above normal arterial blood pressure, to ensure adequate perfusion. Actual perfusion flow was not measured. The vagus nerve was then dissected free of surrounding tissue, carefully lifted into a small circular chamber filled with mineral oil, placed

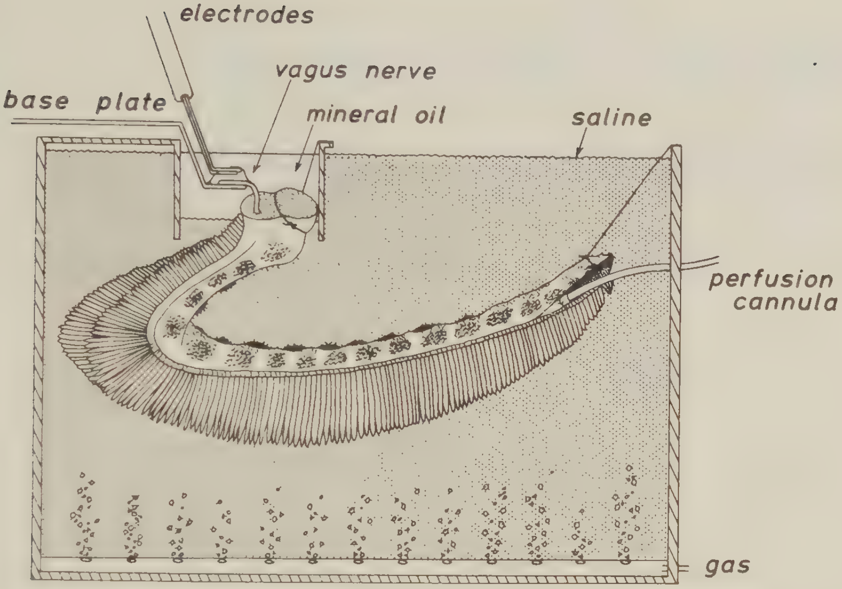

Fig. 1. Schematic diagram of experimental setup for *in vitro* recording of vagal afferent activity from the isolated, perfused gill.

on a dissecting platform (fig. 1) and desheathed. Small filaments were dissected from the distal end of a small cut made in the nerve and single unit action potentials from afferent fibers were recorded by conventional means using bipolar platinum electrodes. The activity was amplified with a Framp* PRA-2 preamplifier (F.M. Smith, Vancouver, Canada) and Grass* P15 differential A.C. amplifier whose frequency bandwidth was set from 30 Hz to 10 kHz. The amplifier output was further filtered with a 60 Hz notch filter. The filtered output from the amplifier was monitored with an oscilloscope and audio amplifier and connected to a W.P.L.* 121 window discriminator. Both the filtered signal and window discriminator output were stored on magnetic tape for later analysis using an instantaneous rate meter (EKEG* Electronics, Vancouver, Canada) and a Gould* Integrating Amplifier averaging ENG activity over 100 msec intervals.

All afferent fibers were initially tested for O_2 sensitivity by lowering the oxygen partial pressure (P_{O_2}) of the bathing solution by bubbling N_2 through the bath. The P_{O_2} of the bathing solution could be slowly lowered in this fashion and restored by again, bubbling with air. Following this procedure the response of each fiber to brief occlusion of the perfusion cannula was determined. All fibers responding to hypoxia invariably showed a dramatic increase in activity during this manoeuver. Finally, the response of most fibers to changes in P_{O_2} of the perfusion fluid produced by bubbling N_2 through the perfusion reservoir, was also measured. Because these experiments were principally designed to test for sensitivity to changes in environmental P_{O_2}, we were restricted in our ability to alter perfusion flow to either on or off and perfusate P_{O_2} to only one level of hypoxia. Perfusion fluid leaving the gill arch via the severed vessels entered the bathing fluid. This led to a slow turn over of the bathing solution throughout the experiment. Although the aeration procedure used to set the P_{O_2} of the bathing solution should have rapidly mixed and equilibrated the perfusion fluid as it left the gill arch, small transient changes in P_{O_2} localized around the distal stub of the gill arch may have occurred. The levels of P_{O_2} in both the bathing and perfusion solutions were measured throughout the experiments using a Radiometer* PHM 71 Acid–Base Analyzer and Oxygen electrode.

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* Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

Recordings were obtained in this study from 86 single units of which 22 exhibited some degree of O_2 sensitivity.

Of the 64 fibers which were not sensitive to changes in P_{O_2} of either the bathing or perfusion solutions, over 20 exhibited a variety of bursting patterns of activity. Such activity varied from bursts of 2 to 3 spikes to bursts of several hundred spikes. As a rule, the larger the burst of activity, the longer the interval between bursts (fig. 2). These fibers did not respond to mechanical stimulation of the gill filaments and gill rakers and thus their normal stimulus modality remains unknown.

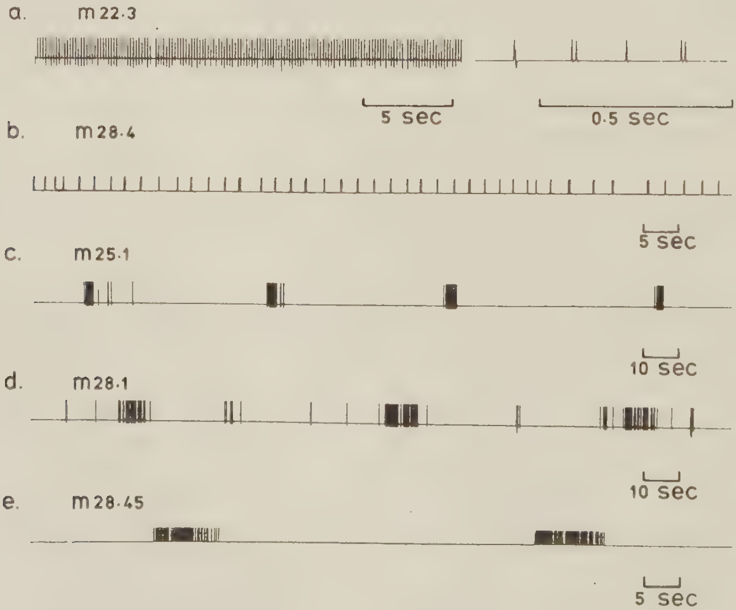

Fig. 2. Electroneurograms of afferent activity from 5 single units (a–e) exhibiting various patterns of bursting discharge under normoxic conditions. Code numbers for each fiber are included on the upper left of each trace for identification.

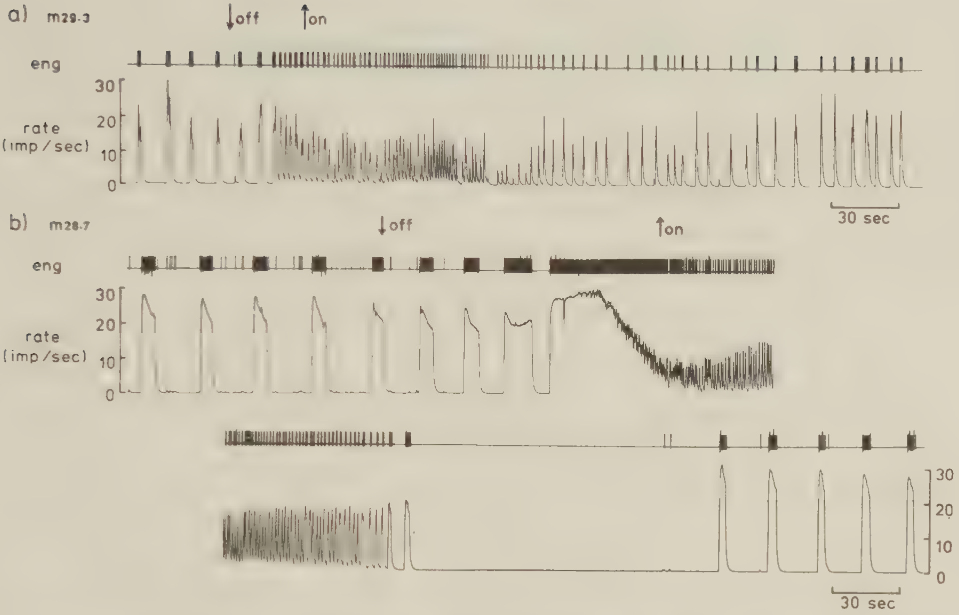

Fig. 3. Electroneurograms and instantaneous discharge rates recorded from 2 fibers exhibiting bursting activity which were sensitive to hypoxia. Perfusion of the gill was turned off and back on at the arrows. The lower two traces for the fiber shown in panel b continue on immediately from the upper two traces.

Five of the 22 fibers which were O_2 sensitive showed similar bursting patterns. The effect of transiently stopping gill perfusion is shown for two of these fibers in fig. 3. Stoppage of flow generally led to a dramatic increase in overall receptor discharge rate brought about by a great increase in burst frequency accompanied by a smaller reduction in the number of spikes per burst. No attempt was made to quantify the responses of these fibers.

The remaining 17 fibers exhibited irregular, low level discharge under normoxic conditions. All fibers exhibited a strong response to temporary occlusion of the perfusion line which could be reproduced by lowering the P_{O_2} of the perfusion fluid (fig. 4a). Six fibers, however, showed no response to a change in the P_{O_2} of the bathing solution as long as perfusion flow and P_{O_2} were maintained (fig. 4b,c). Eleven fibers did respond to a reduction in the P_{O_2} of the bathing solution. Figure 5 illustrates the typical response of one of these fibers to both a lowering of the bath P_{O_2} as well as to a temporary cessation of perfusion. The responses of all eleven, P_{O_2} sensitive fibers are plotted as a function of bath P_{O_2} in fig. 6 and the mean response of these fibers is compared to similar responses measured for cat carotid and aortic bodies (fig. 6, insert).

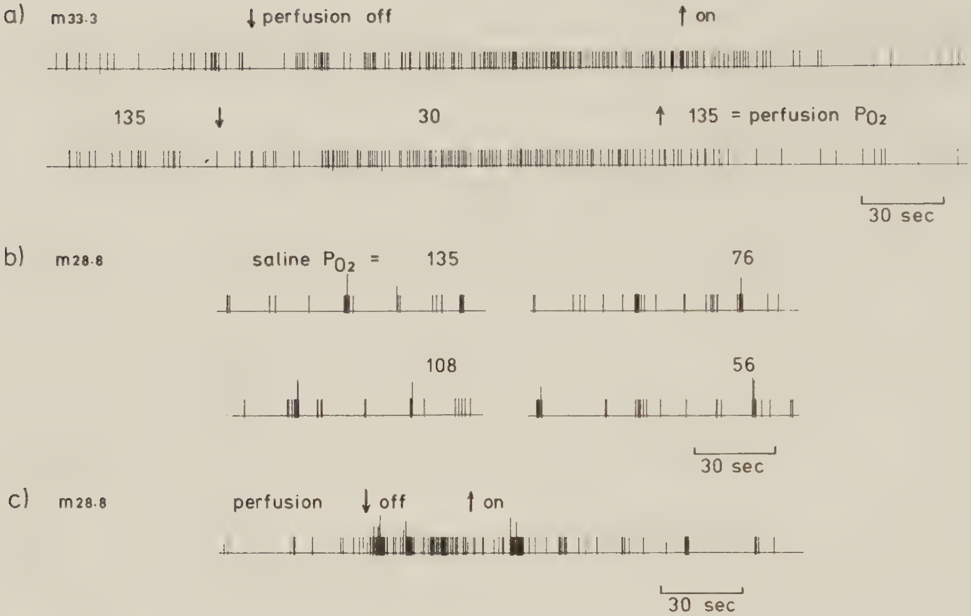

Fig. 4. (a) Electroneurograms of a single unit illustrating the response to temporarily turning perfusion flow off (upper trace) and to changing the P_{O_2} of the perfusion fluid (lower trace). The electroneurograms of a single unit which did not respond to changes in external P_{O_2} are shown in panel b while the response of the same fiber to temporary occlusion of the perfusion line is shown in panel c.

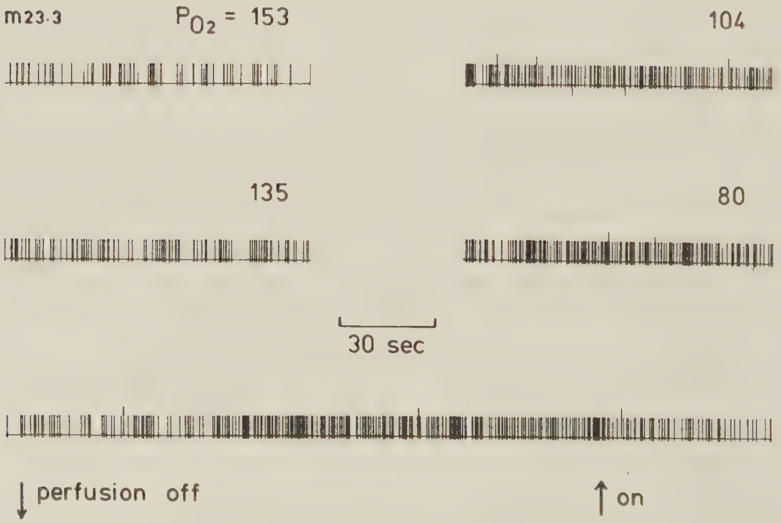

Fig. 5. Responses of a typical unit to changes in external P_{O_2} (levels indicated) are shown along with the response of the same unit to a temporary cessation of perfusion.

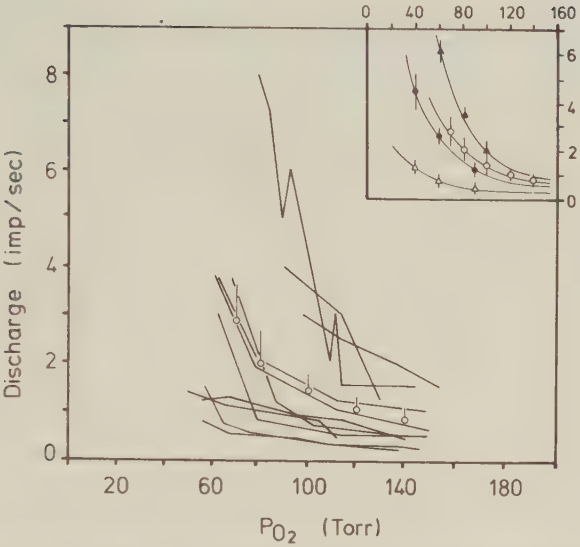

Fig. 6. The changes in discharge of eleven O_2 sensitive units are plotted against changes in external P_{O_2}. Mean values for all fibers are indicated by the open symbols. Insert: the responses of cat carotid body (▲, Mulligan *et al.*, 1981; ●, Lahiri *et al.*, 1981) and aortic body chemoreceptors (△, Lahiri *et al.*, 1981) are plotted along with those of the tuna gill O_2 receptors (○) for comparison. Vertical bars indicate ± 1SE.

Discussion

The results of this study demonstrate the presence of O_2 sensitive receptors in the first gill arch of yellowfin tuna with afferent fibers running in the vagus nerve. We found this nerve extremely sensitive to handling and thus it required more cautious manipulation than similar preparations of the vagus nerve in other vertebrate groups with which we have worked. Although it remains possible that these receptors are particular to tuna or other highly active species of fish, we feel that it was both the size and length of the afferent nerve innervating the first gill arch as well as the fact the fish were equilibrated to room temperature that contributed to the success of this preparation.

The only electrophysiological recordings reported to date of O_2 sensitive changes in afferent information arising from the branchial regions of fish were recorded from vagal branches innervating the pseudobranch in trout (Laurent, 1967, 1969; Laurent and Rouzeau, 1969, 1972). The activity recorded in these studies was characterized by slow (>4 ms), low amplitude voltage changes which were not readily distinguishable from background noise. The authors characterized this discharge as Type B activity as opposed to a Type A activity which consisted of distinct impulses of over 50 μV with spike potentials lasting less than 2 msec. Although the spontaneous pattern of voltage changes associated with Type B activity was irregular under normoxic conditions and changed rapidly with changes in the P_{O_2} of the solution perfusing the pseudobranch, the sensitivity of the response was extremely low, averaging only a 1% change in discharge per Torr P_{O_2} over the range from 10 to 100 Torr P_{O_2}. By comparison, the activity recorded in the present study was of a classical nature, similar to the Type A activity of these earlier workers, and showed a hyperbolic relationship between discharge frequency and P_{O_2}. Although measurements were not obtained at P_{O_2} levels below 60 to70 Torr for most fibers, extrapolation of the relationships obtained at higher P_{O_2} would give a mean sensitivity for these receptors approximately an order of magnitude greater than that recorded from the trout pseudobranch. These response characteristics recorded from the eleven, non-bursting fibers which were sensitive to environmental P_{O_2}, in the present study, are similar to those reported for cat carotid body chemoreceptors over this same range of P_{O_2} (fig. 6, insert) (Lahiri *et al.*, 1981; Mulligan and Lahiri, 1981).

The bursting discharge which was so prevalent in many of the afferent fibers recorded from in this study is intriguing. Although several recordings revealed fibers exhibiting frequent, small bursts of activity, most showed substantial bursts of over 50 spikes, the bursts occurring from 10 sec to 1 min apart. The normal stimulus modality of most of these fibers does not appear to be low O_2 or mechanical deformation of the gill filaments. Fish gills are known to show a high degree of intrinsic vasomotion (Satchell, 1962) and thus a variety of stimuli associated with smooth muscle contraction/relaxation, changes in vessel flow or local changes in blood gas or metabolite concentration remain as possible sources of rhythmic stimuli. Approximately 20% of the bursting fibers recorded from were sensitive to lowered P_{O_2} in either the bathing or perfusion fluids. Whether the bursting phenomena seen in these fibers under normoxic conditions represents a rhythmic change in local perfusion and hence cyclic changes in local P_{O_2}, also remains speculative.

Although the evidence is indirect, the data suggests that the most likely location of the O_2 sensitive receptors recorded from in this study is in close association with the gill vasculature. To begin with, although all O_2 sensitive receptors (bursting and non-bursting) were sensitive to changes in perfusion flow or perfusion fluid P_{O_2}, not all were sensitive to changes in the P_{O_2} of the bathing solution if adequate perfusion was maintained. Secondly, the speed of response of these fibers to changes in perfusion flow or P_{O_2} was extremely rapid, regardless of levels of P_{O_2} of the bathing solution. Their response (when present) to changes in the P_{O_2} of the bathing solution, on the other hand, was generally slow. The rapid and dramatic increase in receptor discharge associated with cessation of perfusion or reduction in perfusion fluid P_{O_2} further suggests that the metabolic rate of receptor cells or surrounding tissue is high and thus local P_{O_2} falls rapidly when perfusion flow decreases. As with the overall sensitivity of these receptors to P_{O_2}, these additional characteristics are also similar to those of mammalian carotid body chemoreceptors (Fidone and Gonzalez, 1986). Taken together with the phylogenetic evidence indicating that the branchial artery supplying the first gill arch in teleosts gives rise to the carotid artery of mammals, this evidence lends strong support to the hypothesis that the O_2 sensitive chemoreceptors located in the first gill arch of teleosts are homologous to the carotid body chemoreceptors of higher vertebrates (Butler *et al.*, 1977).

The rapid ventilatory responses to changes in environmental P_{O_2} exhibited by tench and trout suggests the presence of a chemosensor monitoring environmental P_{O_2} in these species (Eclancher, 1972; Bamford, 1974), while the sluggish response (1–2 min) of *Torpedo* and the sea raven suggest an internal chemosensor (Saunders and Sutterlin, 1971; Hughes, 1978). Other experiments designed to measure the response times to perfusion of presumed reflexogenic zones (Saunders and Sutterlin, 1971) as well as intravascular injection of cyanide or oxygenated and deoxygenated blood (Bamford, 1974; Eclancher and Dejours, 1975) have been equally equivocal. More or less by default, several investigators have concluded that the O_2 receptors lie within the CNS (Saunders and Sutterlin, 1971; Bamford, 1974). The electrophysiological studies of Laurent and co-workers mentioned earlier, as well as histological studies, have implicated the pseudobranch as a site of chemoreceptors involved in control of ventilation in teleosts and elasmobranchs (Laurent, 1967, 1969; Laurent and Rouzeau, 1969, 1972; Barets *et al.*, 1970) but destruction of the pseudobranch in teleosts does not eliminate the respiratory responses to hypoxia (Bamford, 1974). In fact, such responses do not disappear, although they are modified, by transection of the entire 9th and 10th cranial nerves in teleosts (Saunders and Sutterlin, 1971). Thus, until similar studies are performed on tuna, it is not possible to speculate on whether the receptors recorded from in the present study play a role in the ventilatory responses of tuna to environmental hypoxia or not.

The source of receptive sites involved in the cardiac responses to environmental hypoxia are much better delineated. In elasmobranchs they are diffusely scattered throughout the orobranchial and parabranchial cavities and innervated by the 5th, 7th, 9th and 10th cranial nerves (Butler *et al.*, 1977). In teleosts, they appear restricted to the first gill arch and are innervated by the 9th and 10th cranial nerves (Daxboeck and Holeton, 1978; Smith and Jones, 1978; Smith and Davie, 1984). Recent descriptions of a widespread system of neuroepithelial cells in the primary lamellae of all gill arches in teleosts, however, suggest that O_2 sensors may be located more widely than just the first gill arch (Dunel-Erb *et al.*, 1982). Because of limits to the number of fish available for the present study, no attempt was made to record from other branches of the vagus innervating gill arches II to IV in the tuna. The innervation and response characteristics of the receptors recorded from in the first gill arch, however, certainly implicate them as an afferent limb for the cardiac responses shown by this species to environmental hypoxia.

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8669

DEVELOPMENT AND DISTRIBUTION OF LARVAE AND PELAGIC JUVENILES OF OCEAN WHITEFISH, *CAULOLATILUS PRINCEPS*, IN THE CALCOFI SURVEY REGION

H. GEOFFREY MOSER, BARBARA Y. SUMIDA, DAVID A. AMBROSE, ELAINE M. SANDKNOP, AND ELIZABETH G. STEVENS
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

Ocean whitefish larvae occurred in 88 tows taken on CalCOFI plankton surveys from 1954 to 1981. The robust larvae develop a distinctive array of spines and spiny ridges in the head region. The body becomes covered with minute spines, which develop on each scale. Larvae also have a characteristic pattern of melanistic pigmentation, which makes it possible to identify early stages that have not yet developed head spines.

Larvae occurred from Ensenada (CalCOFI line 100) to Magdalena Bay (line 140) and seaward to Guadalupe Island. Occurrences were concentrated off central Baja California; only 20% of the positive tows were north of Sebastian Viscaino Bay. It is apparent from the distribution of larvae that ocean whitefish populations off southern California are recruited from Baja California.

RESUMEN

Larvas oceánicas de *Caulolatilus princeps* estuvieron presentes en 88 arrastres de plancton realizados durante el programa CalCOFI entre 1954 y 1981. Estas robustas larvas desarrollan un claro conjunto de espinas y zonas espinosas en la región de la cabeza. El cuerpo se cubre con espinas diminutas, las cuales crecen sobre cada escama. Las larvas tienen, además, un patrón de pigmentación melánico característico que permite identificar estadíos tempranos que aún no han desarrollado espinas en la cabeza

Se encontraron larvas desde Ensenada (CalCOFI línea 100) hasta Bahía Magdalena (línea 140) y mar afuera de la Isla Guadalupe. Las larvas se concentraron frente a la zona central de Baja California; sólo un 20% de los arrastres con larvas ocurrió al Norte de la Bahía Sebastián Vizcaíno. La distribución de las larvas indica que las poblaciones oceánicas de *Caulolatilus princeps* en el Sur de California son formadas por reclutas provenientes de Baja California.

INTRODUCTION

The ocean whitefish, *Caulolatilus princeps*, ranges from Vancouver Island, British Columbia, to Peru and is a prominent coastal bottomfish off southern California and Baja California (Miller and Lea 1972; Dooley 1978). Southern California commercial passenger fishing boat catch from 1972 to 1983 ranged from 11,000 to 61,000 fish per year, with an average catch of 32,000 fish for the 12-year period[1]. Ocean whitefish ranked tenth in a survey of landings of the southern California private sport fishery (Wine 1978). Commercial landings declined steadily from a catch of 100,000 pounds in 1946 to less than 2,000 pounds in 1956 and have not increased appreciably since (Fitch and Lavenberg 1971). The species is an excellent food fish, and related species in the family Malacanthidae command a high market price, especially in Japan, where they are used for sashimi (S. Kato, National Marine Fisheries Service, Tiburon, California, pers. comm.).

What little is known about the biology of *C. princeps* is summarized in Fitch and Lavenberg (1971). Fourmanoir (1970) briefly described some juveniles taken from tuna and lancetfish stomachs. Kramer and Smith (1973) briefly summarized the distribution of ocean whitefish larvae from CalCOFI surveys of 1955-60. Johnson (1984) summarized rostral spination in *Caulolatilus* larvae in comparison with other malacanthid genera. Detailed descriptions of larvae and juveniles of other malacanthid species (Okiyama 1964; Fahay and Berrien 1981; Fahay 1983) show that in its early life history stages this family is among the most highly developed of all teleosts.

Larvae of *C. princeps* are relatively rare in California Cooperative Oceanic Fisheries Investigations (CalCOFI) plankton collections; however, this may result partly from their distribution off coastal Baja California, where sampling has been relatively low. The purpose of this paper is to describe the larvae and pelagic juveniles of *C. princeps* and summarize their distribution in CalCOFI samples taken during 1954-81.

MATERIALS AND METHODS

A total of 163 *C. princeps* larvae and 8 pelagic juveniles was available for study. Larval specimens ranged from 1.7 mm NL to 7.9 mm SL, and pelagic juveniles ranged from 15.5 to 44.5 mm SL. A developmental series was established to study general morphology,

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[1] Reports of fish caught by the California commercial passenger fishing boat fleet. California Department of Fish and Game, Marine Resources Division, Long Beach.

TABLE 1
Measurements (mm) of Larvae and Pelagic Juveniles of *Caulolatilus princeps*

Station	Body length	Snout-anus length	Head length	Head width	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length
6107 123.45	2.6	1.0	0.59	0.42	0.13	0.27	0.68	0.19	0.19	—
6608 120.45	2.8	1.2	0.65	0.57	0.18	0.33	0.83	0.22	0.31	—
6608 120.45	3.0	1.6	0.80	0.56	0.24	0.33	0.86	0.21	0.37	—
5410 130.55	3.3	1.5	1.0	0.73	0.32	0.38	1.0	0.28	0.35	—
5707 120.35	3.7	1.8	1.1	0.80	0.32	0.40	1.2	0.27	0.48	—
5707 120.35	4.0	1.9	1.2	0.83	0.35	0.47	1.2	0.32	0.57	—
5907 133.45	4.2	2.0	1.2	0.95	0.30	0.48	1.3	0.33	0.62	—
6007 130.35	4.5	2.1	1.3	1.0	0.35	0.58	1.4	0.40	0.65	—
5908 123.55	4.7	2.3	1.5	1.2	0.36	0.60	1.5	0.37	0.64	0.02
5904 137.35	5.0	2.4	1.6	1.2	0.34	0.60	1.6	0.40	0.68	0.03
6107 133.35	5.3	2.7	1.7	1.2	0.30	0.65	1.8	0.50	0.69	0.05
H-5706 120.35	5.7	2.9	1.9	1.2	0.53	0.80	2.1	0.67	0.76	0.06
H-5706 120.35	6.1	3.4	2.2	1.3	0.55	0.87	2.3	0.70	0.82	0.04
5102 140.30	7.1	4.2	2.8	1.7	0.70	1.0	2.9	1.0	1.0	0.43
5302 100.30	7.9	4.7	3.1	1.8	0.93	1.2	3.2	1.3	1.0	0.71
6509 107.40	15.5	9.5	5.6	2.8	1.5	2.1	6.0	—	1.4	—
5706 130.60	16.9	10.0	5.9	3.1	1.6	2.1	6.3	3.0	1.5	2.2
5510 123.50	27.8	17.2	9.2	4.6	1.8	3.2	9.2	4.4	1.9	3.7
7510AX 130.30	33.9	18.8	10.3	5.4	2.2	3.9	10.1	5.8	2.3	4.3
6010B 117.30	44.5	25.8	12.7	6.1	3.2	4.0	12.8	7.5	2.8	6.2

Specimens between dashed lines are in the notochord flexion stage; those below the solid line are pelagic juveniles.

morphometry, and pigmentation. Additional specimens from the collection were used to define variability of these features. Subsequently, the series was stained with Alizarin Red-S and cleared in a graded series of KOH and glycerin to determine the sequence of formation of ossified fin rays, head spines, and scale patches. Most of the small specimens were poorly ossified because of calcium leaching in preservation and, for these specimens, only the appearance of unossified fin rays could be noted. The descriptive methods and terminology follow Ahlstrom et al. (1976) and Moser et al. (1977). Head spines are named for the bones from which they originate. Prior to the completion of notochord flexion, body length is measured from the tip of the snout to the tip of the notochord and is designated "NL." In postflexion specimens body length is measured to the posterior edge of the hypural plate and is termed "SL."

DESCRIPTION

General Morphology

Larvae of *C. princeps* are characterized by a robust body form and the development of larval features at a comparatively small size (Tables 1-3; Figures 1 and 2). Our smallest intact specimen (2.6 mm) has a relatively large head and a compact coiled gut with no evidence of yolk. At the beginning of notochord flexion (about 5.7 mm NL) the larva is highly robust and deep-bodied, with a massive head, triangular-shaped gut mass, and large eye. Notochord flexion is completed at about 7.0 mm SL, and this body form is maintained throughout the postflexion stage. Development of the larval morph is shown by changes in body proportions (Table 2). Relative snout-anus length, head length, head width, snout length, and body depth increase throughout the larval period. Each of these propor-

TABLE 2
Average Body Proportions (% ± Standard Deviation) for Larvae and Pelagic Juveniles of *Caulolatilus princeps*

	Snout-anus length	Head length	Head width	Snout length	Eye diameter	Body depth	Pectoral fin length	Pelvic fin base depth	Pelvic fin length
Stage	Body length	Body length	Head length	Head length	Head length	Body length	Body length	Body length	Body length
Preflexion	47.2 ± 4.05	28.8 ± 3.25	21.6 ± 2.66	25.9 ± 4.30	41.1 ± 4.46	30.6 ± 2.06	7.9 ± 0.70	12.6 ± 2.25	~1.0 ± 0.00
Flexion	53.5 ± 3.54	34.5 ± 2.12	21.0 ± 0.00	26.5 ± 2.12	41.0 ± 1.41	37.5 ± 0.71	11.5 ± 0.71	13.0 ± 0.00	1.0 ± 0.00
Postflexion	59.0 ± 0.00	39.0 ± 0.00	23.5 ± 0.71	27.5 ± 3.54	37.5 ± 2.12	41.0 ± 0.00	15.0 ± 1.41	13.5 ± 0.71	7.5 ± 2.12
Juvenile	59.0 ± 2.74	32.6 ± 3.05	16.6 ± 1.67	24.0 ± 3.32	36.6 ± 3.78	33.6 ± 3.34	17.0 ± 0.82	7.6 ± 1.34	13.2 ± 0.50

TABLE 3
Sequence of Development of Head Spines in Larvae of *Caulolatilus princeps*

Spine	Body length (mm)													
	.2.6	2.8	3.1	3.3	3.7	4.0	4.4	4.7	5.0	5.3	5.7	6.1	7.1	7.9
Preopercle margin—angle	—	+	+	+	+	+	(2)	(2)	(2)	(3)	(6)	B	(6)	(11)
Preopercle margin—upper series	—	1	1	2	2	3	3	3	4	4	4	5	5	6
Preopercle margin—lower series	—	—	1	2	3	3	4	3	4	4	5	5	5	5
Preopercle ridge—upper series	—	—	—	—	—	—	—	—	—	—	1	3	2	4
Preopercle ridge—lower series	—	—	1	1	2	2	4	3	4	4	5	6	6	6
Frontal—1st transverse ridge series	—	—	1	2	3	3	5	5	4	5	6	9	9	9
Frontal—2nd transverse ridge series	—	—	—	—	1	2	3	4	4	5	5	5	8	9
Frontal—3rd transverse ridge series	—	—	—	—	—	2	3	3	3	4	5	B	9	9
Frontal—secondary transverse ridges*	—	—	—	—	—	—	—	—	1	1	2	2	5	5
Frontal—longitudinal ridge series	—	—	—	—	—	1	3	3	3	3	4	B	7	8
Frontal—anterior longitudinal ridge series	—	—	—	—	—	1	2	3	3	4	4	5	5	7
Frontal—supraocular shelf series	—	—	—	—	1	3	4	4	4	6	7	10	10	13
Posttemporal—upper series	—	—	1	3	3	3	4	4	6	7	7	9	10	12
Posttemporal—lower series	—	—	—	—	1	2	2	2	2	4	3	3	5	5
Supracleithrum series	—	—	—	—	—	1	1	1	2	2	3	3	4	5
Dentary series	—	—	—	4	3	6	6	7	6	8	9	12	11	12
Pterotic series	—	—	—	—	—	—	1	1	1	1	2	4	4	5
Interopercle series	—	—	—	—	—	—	1	2	2	2	2	2	2	3
Subopercle series	—	—	—	—	—	—	—	—	—	—	1	1	1	2
Opercle	—	—	—	—	—	—	—	—	—	—	1	1	1	1
Nasal—lateral series	—	—	—	—	—	—	—	—	1	2	3	4	6	7
Nasal—median series	—	—	—	—	—	—	—	—	—	2	3	4	4	4
Nasal—ventral series	—	—	—	—	—	—	—	—	—	—	1	1	3	3
Lacrimal—upper series	—	—	—	—	—	—	—	—	—	—	4	4	6	8
Lacrimal—lower series	—	—	—	—	—	—	—	—	—	—	3	6	6	9
Extrascapular—upper series	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Extrascapular—lower series	—	—	—	—	—	—	—	-	—	—	—	—	1	2

*Number of ridges indicated, not the number of spines.

Numbers of spines in each series are listed. Spinules on preopercular angle spine are enclosed in parentheses. Symbols: + = present; B = broken.

tions, except relative snout-anus length, decreases in pelagic juveniles as the body becomes more streamlined.

Larvae of *C. princeps* develop a remarkable array of head spines. Preopercular spines develop in larvae less than 3.0 mm NL. The spine at the angle of the preopercle develops first, then spines are added above and below it throughout the larval period (Table 3; Figures 1 and 2). The angle spine develops prominent spinules late in the larval period. A second preopercular series forms on a ridge anterior to the preopercular margin.

Numerous spinous ridges develop on the frontal bone. Each begins with one or two broad-based spines and gradually adds spines to form a serrate ridge. Initially a transverse ridge forms above the eye; two additional transverse ridges form posterior to it, and two longitudinal ridges form anterior to it. Later in the larval period several secondary transverse ridges develop anterior to the original three; these curve forward to form a pattern that appears heart-shaped from dorsal view. The longitudinal ridges become aligned with the lateral ridges of the nasal bone. These series of ridges are joined anteriorly by a transverse ridge at the point of fusion of the nasal bones to form a long troughlike structure that projects beyond the upper jaw. In addition to these ridges, a spinous supraocular shelf forms at the margin of the frontal bone and projects laterally over the eye. A spinous ridge develops on the pterotic bone posterior to the supraocular shelf, and, late in the larval period, ridges develop on the extrascapular bone in the epiotic region (Table 3; Figures 1 and 2).

Ornate spinous ridges develop on the posttemporal and supracleithral bones early in the larval period. The upper series on the posttemporal forms first and becomes antlerlike at full development (Table 3; Figures 1 and 2). The lower posttemporal and supracleithral ridges are less ornate, and fuse to form a continuous structure.

Ventrally on the head, spinous ridges develop on the upper and lower margins of the lacrimal bone and along the ventral margin of the dentary bone. Two spines form on the subopercle, three form on the inter-

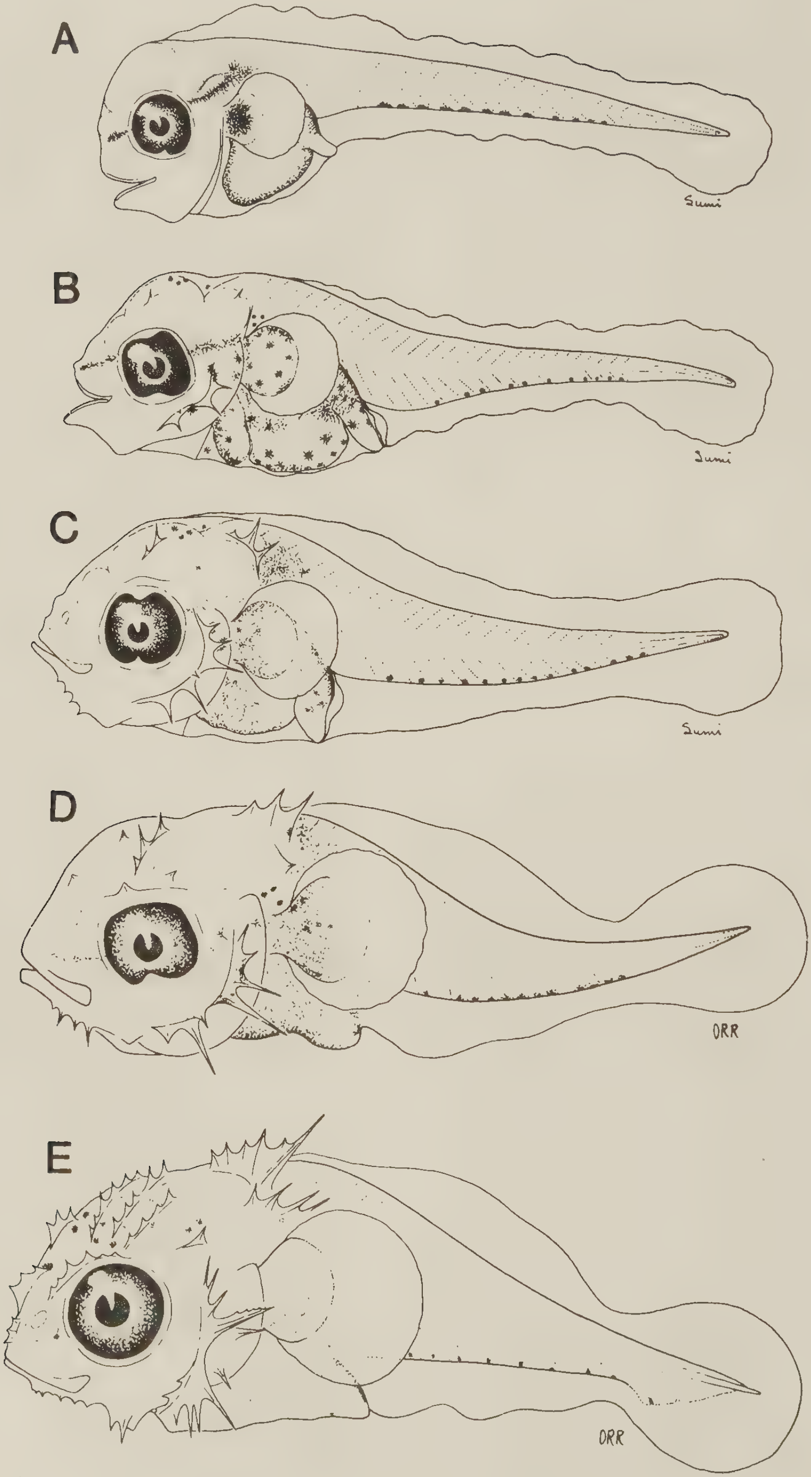
A
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Figure 1. Preflexion larvae of *Caulolatilus princeps*: (*A*) 2.6 mm; (*B*) 3.0 mm; (*C*) 3.3 mm; (*D*) 3.8 mm; (*E*) 5.3 mm.

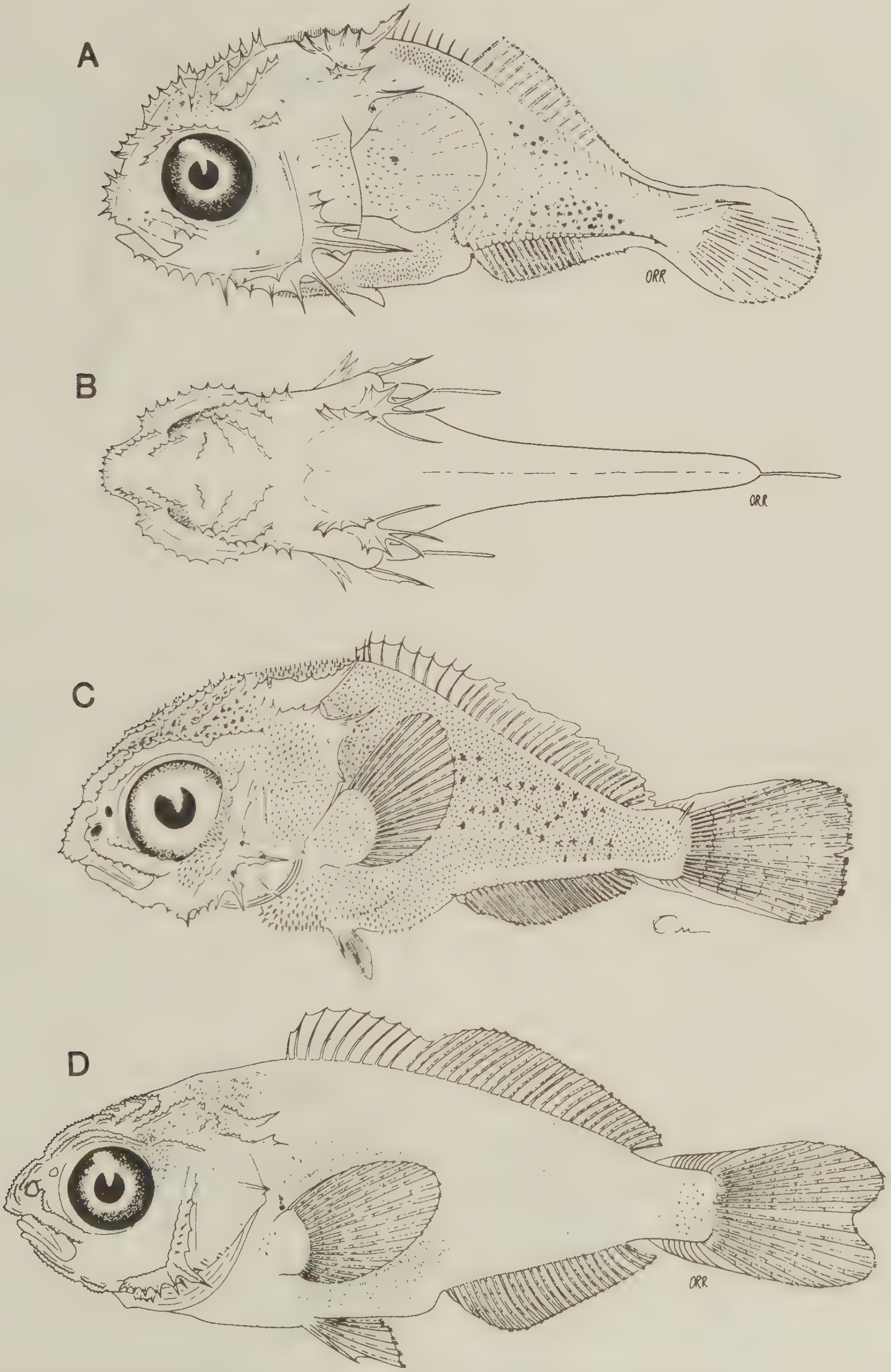

Figure 2. Developmental stages of *Caulolatilus princeps:* (*A*) 6.2-mm larva, flexion stage; (*B*) 6.2-mm larva, dorsal view; (*C*) 7.9-mm larva; (*D*) 16.8-mm pelagic juvenile.

TABLE 4
Meristics of Stained Specimens of *Caulolatilus princeps*

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchio-stegal rays		Pectoral fin rays		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right			Left	Right	
3.7	—	—	—	—	1	1	—	—	—	—	—	—	—
4.0	—	—	—	—	4	4	—	—	—	—	—	—	—
4.1	—	—	—	—	3	3	—	—	—	—	—	—	—
4.2	—	—	—	—	4	4	—	—	—	—	—	—	3
4.4	—	—	—	—	5	5	—	—	—	—	—	—	6
4.5	(1)	(1)	—	—	5	5	—	—	—	—	—	—	7
4.7	(1)	(1)	—	—	5	5	—	—	—	—	—	—	7
5.0	(1)	(1)	—	—	5	5	—	—	—	—	—	—	9
5.1	(4)	(4)	—	—	6	6	(6)	(5)	(7)	(VIII,4)	—	—	13
5.3	4	4	—	—	6	6	(5)	(5)	(7)	(VIII,5)	—	—	14
5.7	(6)	(6)	—	—	6	6	(7)	(7)	(I,12)	(VIII,10)	—	—	15
6.1	(8)	(7)	—	—	6	6	—	(12)	(I,17)	(IX,17)	—	—	17
7.1	9	8	—	—	6	6	12	12	II,22	IX,20	I,3	I,3	27
7.9	9	8	4	4	6	6	19	19	II,25	IX,24	I,5	I,5	—
15.5	9	8	13	11	6	6	19	19	II,25	IX,24	I,5	I,5	—
16.8	9	8	11	11	6	6	18	18	II,24	IX,25	I,5	I,5	—
17.1	9	8	12	12	6	6	19	19	II,25	IX,26	I,5	I,5	—
38.6	9	8	13	12	6	6	19	19	II,25	IX,26	I,5	I,5	—

Specimens between dashed lines are undergoing notochord flexion. Numbers in parentheses indicate unstained fin elements.

opercle, and the opercle has one. In pelagic juveniles the spines on the ridges become less prominent, but the ridges increase in number as multiple ridges develop at the supracleithral shelf, lacrimal, dentary, and preopercular bones.

In addition to head spines, larvae of *C. princeps* develop spinous scales on the head and body. These appear initially in flexion-stage larvae as patches of small conical spines lacking the ossified scale. Flexion-stage larvae develop the following patches: (1) a linear patch on each side of the nape, (2) a linear patch on each side of the spinous dorsal fin, (3) a patch on the opercle, (4) one on the outer surface of the pectoral fin base, (5) one on the ventral midline posterior to the isthmus, (6) a rounded patch on the posteroventral surface of the gut, (7) an elongate patch on the trunk extending posteriad along the midlateral region of the tail. All of these patches enlarge in postflexion larvae, and the supporting scales become ossified. The patches at the nape and fin base enlarge to fill in the body region above the lateral line; the trunk patch enlarges to fill in the area below the lateral line. The gut patch extends anteriad and dorsad to cover the gut area, and the ventral midline patch expands in a broad triangular shape to cover that region. A patch also forms on the cheek posterior to the eye.

In early pelagic juveniles the entire body is covered with scales that have one to several spines located on their posterior regions. The head is also covered, except for the frontal ridge region and the ventral region. In late-stage pelagic juveniles each scale has typically 4-6 spines in a cluster at the posterior central region of the scale.

Fin Formation/Meristics

The first elements to ossify are the branchiostegal rays at about 3.7 mm NL (Table 4). Specimens larger than 5.0 mm NL have the full complement of 6 branchiostegal rays. The sequence of initial ossification of fin rays could not be determined because of calcium leaching during preservation; however, the appearance of unstained rays could be noted, and these are indicated in Table 4. Principal caudal rays appear at about 4.5 mm NL, and the full complement of 9 + 8 rays is present in early preflexion larvae. Procurrent caudal rays begin forming late in the postflexion stage; the full complement is formed in pelagic juveniles (Table 4). Dorsal and anal fin rays appear in 5-mm larvae, and the full complements (D. VIII-IX, 23-26; A. I-II, 23-25) are present in our largest larva (7.9 mm SL).

The pectoral fins have a large rounded base and blade in preflexion larvae. Rays begin to form in 5-mm larvae and are fully formed by the end of the larval period. The pelvic fins are the last to develop and are fully formed in postflexion larvae (Table 4). Vertebrae begin to ossify in 4-mm larvae; all centra (27) are ossifying by the end of the notochord flexion.

Pigmentation

The melanistic pigment pattern present on the smallest larvae of *C. princeps* persists throughout most of the larval period. Melanophores cover all surfaces of the gut and continue dorsally and internally to the anterior region of the trunk (Figure 1). The trunk pigment continues internally through the otic region to the base of the neurocranium and extends forward to the snout. Before the larvae reach 3.0 mm NL, melanophores appear on the nape region, the lateral and medial surfaces of the pectoral fin base, the preopercular-opercular region, the cardiac region, and on the optic and cerebellar lobes of the brain. Pigment on all of these regions intensifies during the remainder of the larval period.

A postanal series of melanophores along the ventral midline is present in the smallest larvae available (Figure 1). The series begins on the third to fifth postanal myomere and extends posteriad to the caudal fin anlage. There are typically 11-14 melanophores in the series; occasional specimens have as few as 9. At the end of the preflexion stage, the hypaxial musculature begins to mask the anterior melanophores in the series; coalescence further reduces the number so that they are not visible in specimens larger than 7.0 mm SL.

The principal change in pigmentation during later larval stages is the gradual posteriad extension of the trunk pigment to cover the entire body. This begins at about 5.0 mm NL, when the region dorsal to the gut becomes covered with large melanophores. This melanistic sheath extends posteriad to about half the distance to the caudal fin in flexion-stage larvae. The pigment sheath covers the entire body posteriad to the hypural region in the largest larva (7.9 mm SL). At this stage only the ventral region of the head and the jaws are unpigmented. The hypural region is fully pigmented in 40-mm juveniles.

DISTRIBUTION

A total of 88 occurrences of *C. princeps* larvae can be documented for CalCOFI plankton surveys during 1954-81. All but 10 of these are from the 1954-69 period, when coverage of the stations off central and southern Baja California was most complete. Ocean whitefish larvae were not identified in survey collections from 1951 through 1953; however, 7 large larvae were found in these collections during the present study. The paucity of occurrences in the surveys of 1972, 1975, and 1978 reflects the limited station coverage in central and southern Baja California during the summer months.

Larvae of *C. princeps* were taken as far north as Ensenada, Baja California, (CalCOFI line 100) and south to Magdalena Bay, Baja California, (CalCOFI line 140). Lack of larvae from stations south of line 140 reflects the infrequent occupancy of stations on CalCOFI lines 143-157. The fact that only 20% of the occurrences were north of Sebastian Viscaino Bay emphasizes the warm-water affinity of ocean whitefish. Larvae were concentrated in a band within about 100 miles of the coast, although some were found at nearly twice that distance—as far seaward as station 70 on some lines (Figure 3). Pelagic juveniles were even more closely associated with the coast.

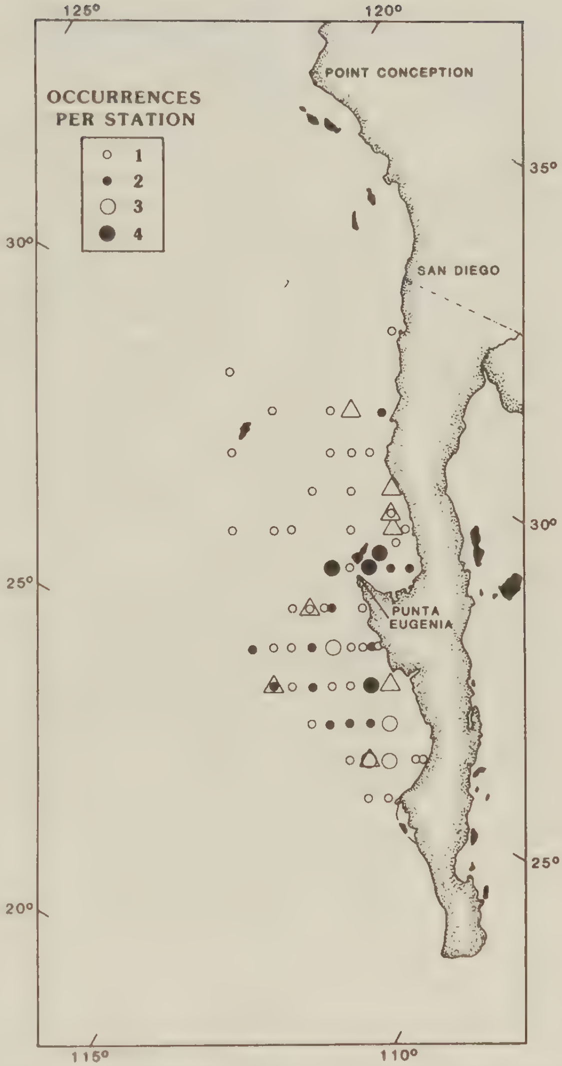

Figure 3. Pooled numbers of occurrences of *Caulolatilus princeps* larvae (circles) and pelagic juveniles taken in standard CalCOFI tows from 1954 to 1981. Triangles indicate single occurrences of pelagic juveniles.

Larvae occurred principally in summer: 33% of the occurrences were in July, 25% in August. Larvae were taken in all other months except December, with the number of occurrences ranging from two to eight. Juvenile occurrences were highly clustered seasonally, with 6 of the 8 specimens coming from October cruises.

The number of specimens per tow was small ($\bar{x} = 1.85 \pm 2.69$SD), with 72% of the positive tows represented by a single larva. Larval size ranged from 1.7 mm NL to 7.9 mm SL ($\bar{x}$ = 4.3 mm NL ± 1.093SD), with a paucity of postflexion specimens: only 9 of the 126 measured specimens were larger than 6.0 mm SL. The 8 pelagic juveniles were taken on separate tows; their length measurements were 15.5, 16.8, 17.1, 27.8, 33.9, 38.6, 43.2, and 44.5 mm SL.

It is apparent from the distribution of ocean whitefish larvae that populations in southern California, and perhaps northern Baja California, are recruited from central and southern Baja California. This pattern is seen in other transboundary species like white seabass, yellowtail, and bonito. Although ocean whitefish larvae do not occur off southern California, adults of this population may contribute to production of larvae off central and southern Baja California by periodic migration. Alternatively, they may spawn unsuccessfully in southern California or may be reproductively inactive. A study of the seasonal changes in the gonads of southern California ocean whitefish could solve a part of this puzzle.

ACKNOWLEDGMENTS

The initial identification of ocean whitefish larvae was made by Elbert H. Ahlstrom. H. Orr provided illustrations for Figures 1D and E and 2A-D. Richard Charter helped with the CalCOFI data base.

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8670

Physical oceanographic observations, Antarctic Marine Ecosystems Research in the Ice-Edge Zone program, March 1986

R.D. Muench

Science Applications International Corporation
Bellevue, Washington 98005

D.M. Husby

Pacific Environmental Group
National Marine Fisheries Service/
National Oceanic and Atmospheric Administration
Monterey, California 93940

Temperature and salinity observations were carried out in the northwestern Weddell Sea marginal ice zone (MIZ) during March 1986 as part of the Antarctic Marine Ecosystems Research in the Ice-Edge Zone (AMERIEZ) project. The purpose of these observations was to define the oceanic temperature, salinity, and density fields. Particular emphasis was placed on features, such as vertical stratification in the upper ocean layers, which were expected to impact local biological processes.

The observations were carried out from two vessels. One, the U.S. Coast Guard icebreaker *Glacier,* operated at and within the ice edge. The second vessel, the R/V *Melville,* operated in the open water seaward of the ice edge. Observations from both vessels were made using Neil Brown Mark IV CTD (conductivity/temperature/depth) profiling systems. During the March 1986 program, 66 CTD stations were occupied from the *Glacier* and 49 from the *Melville.* Geographical locations of these stations are shown on figure 1. Most of the CTD casts extended downward to depths greater than 500 meters; more than half of them extended to 1,500 meters.

The study area was characterized by three major water masses, each identifiable based upon its temperature and salinity characteristics (figure 2). (See, for example, Carmack 1977.) The uppermost layer was the surface water. During the March AMERIEZ program, the temperature of this layer was at or near the freezing point (about -1.8°C), where it underlay the sea ice and increased up to about -0.2°C some 200 kilometers east of the ice edge. Salinities varied from 33 to 34 parts per thousand; the higher salinities occurred in areas where freezing was occurring. The layer was vertically well mixed and varied in thickness from less than 25 meters to greater than 40 meters.

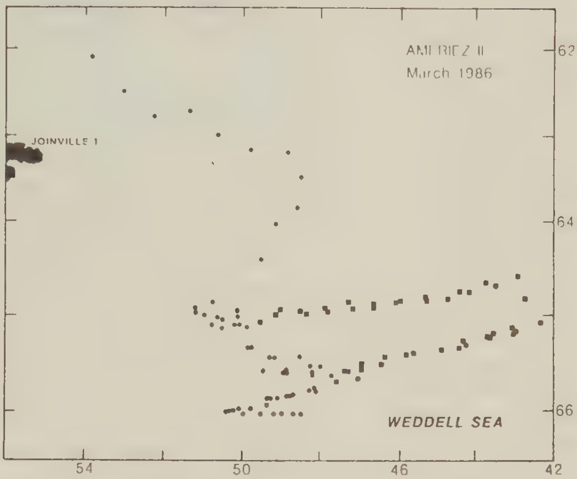

Figure 1. Locations of CTD Stations occupied by U.S. Coast Guard Icebreaker *Glacier* (circles) and R/V *Melville* (squares) during the March 1986 AMERIEZ field program. Arrow indicates approximate location of station shown in figure 2.

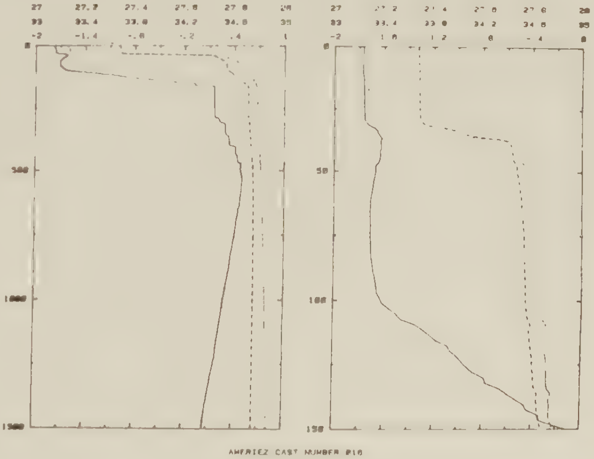

Figure 2. Vertical profiles of temperature (solid curves), salinity (dashed curves), and density as sigma-t (dotted curves) derived from a CTD station taken near the ice edge during the March 1986 AMERIEZ program. Left-hand plot shows mid-depth step structures, which are especially pronounced in temperature, and right-hand plot shows upper layer detail. Depths are in meters. Station location is indicated on figure 1.

Underlying the surface water all locations was the Weddell winter water. This layer reflected cooling and freezing which occurred during the preceding winter and had temperatures between about -1.5° and -1.7°C and a salinity of about 34.5 parts per thousand. The winter water extended from just beneath the surface water to about 100 meters and was separated from the upper waters by a region of very strong vertical gradients in temperature, salinity, and density. A weak (0.1°–0.2°C) temperature maximum layer 10–20 meters thick was often present between the surface and winter water layers. This thermal feature was a remnant due to absorption of incoming solar radiation during the preceding summer.

The deepest water mass observed was the Weddell warm water, which extended from the bottom of the winter water at about 100 meters to more than the 1,500 meters maximum cast depths. Temperatures in this layer varied between 0°C and 0.5°C, and salinities were 34.65 parts per thousand at the upper boundary of the layer increasing to 34.7 parts per thousand at the greatest observed depths. The greatest observed temperatures in this layer occurred at about 500 meters depth. The region between this temperature maximum and the top of the layer at about 100 meters was characterized, over much of the study region, by large (more than 100 meters in vertical extent) temperature and salinity steps. These features have also been noted by Middleton and Foster (1980). There is as yet no satisfactory explanation for their presence, though they may play a significant role in vertical heat fluxes.

Dynamic heights relative to the 1,500-decibar level were computed to estimate whether appreciable baroclinic circulation was present over the study region. The total dynamic relief was of the order of only a few dynamic centimeters over the entire area, indicating that the baroclinic circulation was negligible.

During the field program, two separate "rapid transects" were occupied by both vessels. There were attempts to sample along transects over time intervals which were short relative to the periods over which changes might be expected to occur in the water column. No significant variations were detected between occupations of these transects, suggesting that the physical system was reasonably steady-state during the 30-day duration of the cruise.

Finally, no strong horizontal gradients, or frontal systems, were observed. This was in contrast to the AMERIEZ I program, which sampled in November 1983 along the strong frontal system separating the outflowing Weddell Sea water from the waters of the Eastern Scotia Sea. The region sampled during the March 1986 program was characterized only by very gradual horizontal variation—primarily in the upper layers, in moving from west to east away from the sea-ice edge.

The northwestern Weddell Sea MIZ region was intensively sampled, revealing three water masses: the Weddell surface water, the Weddell winter water, and the Weddell warm water. The dominant upper layer feature was the widespread surface water layer, which was underlain by very strong vertical gradients. Such gradients imply that little vertical mixing is occurring through the bottom of the upper layer. The dominant deep feature was the presence of vertical temperature steps which may be related to region-wide vertical heat transfer.

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8671

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Fishery Resources Surveyed with Deep-Sea Camera

by Bruce C. Mundy

■ A recently acquired deep-sea camera was used to survey fishery resources at Penguin Bank, off Moloka‘i, said Richard S. Shomura, director of the Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service (NMFS). The camera was set on the ocean floor in 404 feet of water during a cruise of the NOAA ship *TOWNSEND CROMWELL* completed on April 18. Surveys were conducted near areas where three artificial reefs had been placed by the NMFS. Bait placed in front of the camera attracted animals from the surrounding water to the place where they were photographed. The camera, prepared by NMFS fishery biologist John T. Harrison, took a picture every minute for 2 hours. Although ‘aweoweo were the only food fish attracted to the camera, other fish, such as puffer and eel, and crab were attracted to the bait. Small shrimp were seen in almost every photograph. The shrimp, which are too tiny to be used as food directly by man, may be an important energy source for commercially valuable fish. The deep-sea camera, allowing views of areas difficult to see with divers or to sample with nets, will be a useful tool for future research by the NMFS. The camera can be set at depths as great as 20,000 feet.

Under the supervision of chief scientist Bruce C. Mundy, the *TOWNSEND CROMWELL* cruise also included trap surveys at the Penguin Bank area and studies of the distribution of larval fish near O‘ahu. Fish, shrimp and lobster traps were set in the vicinity of the artificial reefs to determine what types of animals were in the area. While previous observations of the reefs from the University of Hawaii's submersible *MAKALI‘I* have revealed concentrations of fish at the reef, little is known about the numbers of animals on the surrounding bank. The recently completed trap survey found no commercial-sized shrimp and few lobster, crab or fish. Most of the fish were ta‘ape, an abundant species initially introduced to Hawai‘i in 1955.

The third of four planned studies of the distribution of larval fish at O‘ahu was also completed during the cruise; studies have been done during the autumn, winter and spring. The goal of this work is to better understand how the larvae, the very youngest stages of fish, might be affected by Ocean Thermal Energy Conversion (OTEC) power plants planned for the islands. . . . **Bruce**

8672

The Potential Impact of Ocean Thermal Energy Conversion (OTEC) on Fisheries

EDWARD P. MYERS
Ocean Minerals and Energy Division,
Office of Ocean and Coastal Resource Management,
National Ocean Service, NOAA,
Page 1 Building, Room 105,
2001 Wisconsin Avenue NW,
Washington, D.C. 20235

DONALD E. HOSS
DAVID S. PETERS
Southeast Fisheries Center,
Beaufort Laboratory,
National Marine Fisheries Service, NOAA,
Beaufort, NC 28516-9722

WALTER M. MATSUMOTO
MICHAEL P. SEKI
RICHARD N. UCHIDA
Southwest Fisheries Center,
Honolulu Laboratory,
National Marine Fisheries Service, NOAA,
2570 Dole Street,
Honolulu, HI 96822-2396

JOHN D. DITMARS
ROBERT A. PADDOCK
Energy and Environmental Systems Division
Argonne National Laboratory
Argonne, IL 60439

ABSTRACT

The commercial development of ocean thermal energy conversion (OTEC) operations will involve some environmental perturbations for which there is no precedent experience. The pumping of very large volumes of warm surface water and cold deep water and its subsequent discharge will result in the impingement, entrainment, and redistribution of biota. Additional stresses to biota will be caused by biocide usage and temperature depressions. However, the artificial upwelling of nutrients associated with the pumping of cold deep water, and the artificial reef created by an OTEC plant may have positive effects on the local environment.

Although more detailed information is needed to assess the net effect of an OTEC operation on fisheries, certain assumptions and calculations are made supporting the conclusion that the potential risk to fisheries is not significant enough to deter the early development of OTEC. It will be necessary to monitor a commercial-scale plant in order to remove many of the remaining uncertainties.

INTRODUCTION

Under the Ocean Thermal Energy Conversion (OTEC) Act of 1980, the National Oceanic and Atmospheric Administration (NOAA) was given responsibility for licensing U.S. commercial OTEC operations and determining the potential environmental effects associated with this development and operation. NOAA (1982), in an environmental research plan required by the Act, identified two high-priority research areas that could be addressed with the available resources:

1. Determining the region of influence of an OTEC operation on mixing and redistribution of water masses, and
2. predicting the potential effects on fisheries.

Research in the first area has resulted in development of a model to predict the spatial scale and degree of perturbation to ocean waters (Wang 1984). This development responds to a direct licensing requirement of the Act and, in addition, has resulted in information useful in the determination of biological effects.

The second area, prediction of potential fishery effects, was considered a high priority because of the commercial and recreational value of fisheries and because of NOAA's responsibilities for fisheries through the National Marine Fisheries Service (NMFS). In fact, in its environmental research plan for OTEC, NOAA (1982) noted that the ''Achilles heel,'' if any, to OTEC siting and operation could well be the effect on fisheries or other biologically important resources such as corals.

The concern over fisheries is primarily related to the entrainment and impingement that would result with the pumping of large volumes of seawater through an OTEC plant, the secondary entrainment caused by the discharge of OTEC waters, the use of biocides, and the redistribution of ocean properties (e.g., nutrients, trace metals, heat). The very presence of an OTEC structure might add to these factors due to the attraction or avoidance of fish and other biota to OTEC structures. There are other potential problems (NOAA 1981a), e.g., the leakage or spilling of working fluids to the environment, that are not discussed in any detail in this report. The report has focused on those problems associated with the normal everyday operating conditions of an OTEC plant.

NOAA believed that there was much information available that would be useful in making preliminary estimates of OTEC effects on fisheries. This includes information on the oceanographic characteristics of marine waters near potential OTEC sites, on the fates and effects of substances such as biocides, trace metals, and nutrients, and on other problem areas such as entrainment and impingement. Some of this available information is rather general, some site-specific, and some related to experiences from the operation of conventional and nuclear power plants.

A synthesis of pertinent information to assess the potential effects on fisheries was initiated in FY 1982 and culminated in this report. The effort focuses on the Caribbean and the North Pacific, since these are regions where U.S. OTEC interests have the greatest potential for development. It also emphasizes the nearshore application of OTEC more than the open-ocean case. The rationale for this emphasis is that at the present time there appears to be more interest in the nearshore application of OTEC, and there is definitely more reason for concern over the coastal areas as compared to the open ocean, at least during the early development of OTEC.

BACKGROUND

The OTEC Principle

Ocean thermal energy conversion (OTEC) is a renewable energy technology which produces power using a heat engine driven by the temperature difference between warm surface ocean waters and cold deep ocean waters (Gritton et al. 1980). The heat engine can take the form of a closed-cycle process (Fig. 1) which employs a working fluid (e.g., ammonia or Freon™) which is evaporated by warm seawater. The expanding gas drives a gas turbine, is then recondensed by cold seawater, and the process is repeated. The open-cycle process is quite similar to the closed-cycle process, with the exception that the warm seawater, acting as the working fluid, is flash-evaporated and the resulting vapor passed through a turbine. A big advantage of the open-cycle process is that the condensate can be used as a freshwater source.

There are several possible locations and construction strategies proposed for OTEC plants. The plants could be land-based, be mounted or moored on the continental shelf, or be open-ocean plantships (NOAA 1981a). A land-based plant would be constructed onshore with the needed warm-water, cold-water, and discharge pipes extending offshore to reach the desired intake and discharge conditions. A plant mounted on the continental shelf might be similar to an offshore oil rig. A moored plant would be a floating plant that is moored (anchored) to the seafloor. All of the above designs could be used to supply baseload electricity to existing electrical grids. A plantship, on the other hand, would be a ship equipped with an OTEC plant and could utilize suitable thermal resources wherever they existed. The power produced by a plantship could be used to produce energy-intensive products such as hydrogen, ammonia, and methanol (Francis and Dugger 1980; NOAA 1981a; Dugger et al. 1982; Avery et al. 1985).

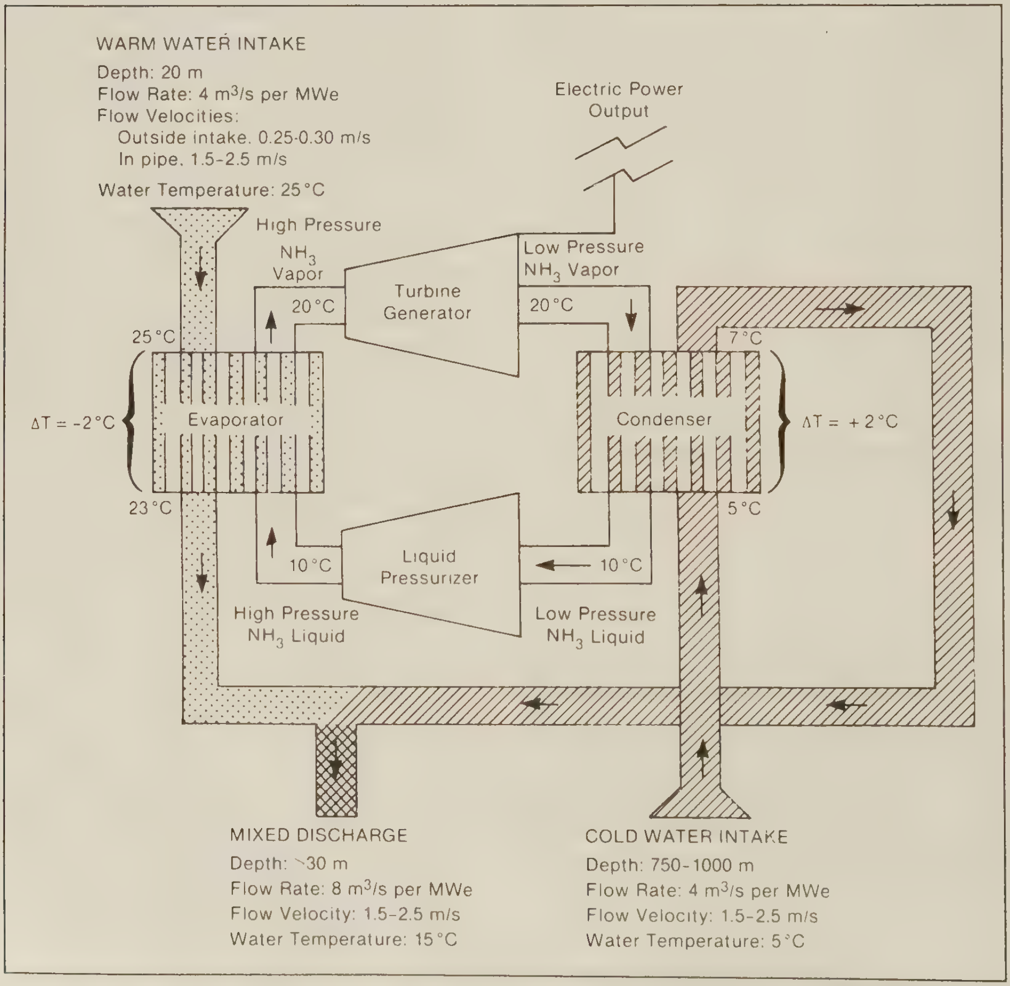
WARM WATER INTAKE
Depth: 20 m
Flow Rate: 4 m3/s per MWe
Flow Velocities:
Outside intake. 0.25-0.30 m/s
In pipe. 1.5-2.5 m/s
Water Temperature: 25°C
Electric Power Output
High Pressure NH3 Vapor
Low Pressure NH3 Vapor
Turbine Generator
20°C
20°C
25°C
7°C
ΔT = -2°C
Evaporator
Condenser
ΔT = +2°C
23°C
5°C
10°C
Liquid Pressurizer
10°C
High Pressure NH3 Liquid
Low Pressure NH3 Liquid
MIXED DISCHARGE
Depth: ~30 m
Flow Rate: 8 m3/s per MWe
Flow Velocity: 1.5-2.5 m/s
Water Temperature: 15°C
COLD WATER INTAKE
Depth: 750-1000 m
Flow Rate: 4 m3/s per MWe
Flow Velocity: 1.5-2.5 m/s
Water Temperature: 5°C

Figure 1.—Schematic diagram of a closed-cycle OTEC system. (adapted from U.S. Department of Energy 1979). (Note: Newer designs can achieve somewhat higher temperature changes across the heat exchangers with slightly less flows; Avery 1984).

Application

A temperature difference of approximately 20°C is needed to make the OTEC process sufficiently efficient to be cost-effective (Myers and Ditmars 1985). Such temperature differences exist between the ocean surface and depths of about 1000 m in most coastal and open-ocean areas within about ±20° of the Equator, and in some areas outside of this band (United Nations 1981). These areas include approximately 70 developing nations with an adequate thermal resource (Table 1). Although temperature differences represent only one of the various forms of renewable ocean energies (e.g., biomass, waves, tides, currents, salinity gradients), it has been concluded that this form of ocean energy potential offers much promise by the year 2000 (United Nations 1981).

Countries that presently have an interest in developing OTEC technology include the United States, France, Japan, Sweden, and the Netherlands. The U.S. Department of Energy has supported design studies for a 40 megawatt-electric (MWe) pilot plant that would be located at Kahe Point, Oahu, Hawaii. During the conceptual design phase of this work, two closed-cycle designs were under development: An artificial island design by Ocean Thermal Corporation (OTC) (1983) that would be located about 550 m offshore, and a tower-mounted concept by General Electric (1983) to be located about 2200 m offshore. The OTC plant was chosen over that of General Electric for the second phase of the project—preliminary design. The OTC plant would utilize the thermal discharge from the Hawaiian Electric Company's (HEC0) conventional power plant at Kahe Point to supplement the thermal resource of the ambient seawater. The intake of ambient warm water would be near the surface at the plant with the intake of cold water further offshore at a depth of about 700 m. Both warm and cold waters, once used, would be discharged as a mixture at a depth of about 100 m.

The French government has been performing preliminary studies related to a 5-MWe prototype open-cycle plant in Tahiti. Japanese companies have designed, built, and operated a land-based closed-cycle 100-kWe plant for the island of Nauru in the North Pacific. Although this demonstration plant has been shut down, there are plans for a 2.5-MWe plant at the same site. Sweden's interest has principally been in building plants or components of plants and selling to developing countries. For instance, they have had discussions with Jamaica for a plant. Certain Dutch companies have similar interests.

U.S. Legislation

Two legislative acts were passed by Congress in 1980 to facilitate the commercial development of OTEC: The Ocean Thermal Energy Conversion Research, Development, and Demonstration Act; and the Ocean Thermal Energy Conversion Act of 1980. The purpose of the OTEC Research, Development, and Demonstration Act (P.L. 96-310) is to accelerate OTEC **technology** development; the designated lead agency is the U.S. Department of Energy. The purpose of the OTEC Act of 1980 (P.L. 96-320) was to create a **legal regime** that would facilitate the commercialization of OTEC in a manner compatible with the protection of the marine environment and other marine resources; the lead agency is the National Oceanic and Atmospheric Administration.

Table 1. Some developing nations with adequate ocean thermal resources (after United Nations 1981)

Region/nation	Lat.	Long.	ΔT (°C) 0-1000 m	Distance from resource to shore (km)
Africa				
Angola	6°S-18°S	11°E-14°E	18-22	65
Benin	6°N	3°E-4°E	22-24	50
Congo	4°S-5°S	22°E-12°E	20-22	50
Gabon	2°N-4°S	9°E-22°E	20-22	50
Ghana	5°N-6°N	3°W-1°E	22-24	50
Guinea	9°N-11°N	24°W-15°W	20-22	80
Guinea-Bissau	11°N-13°N	15°W-17°W	18-19	60
Ivory Coast	5°N	3°W-8°W	22-24	30
Kenya	2°S-5°S	34°E-41°E	20-21	25
Liberia	5°N-17°N	8°W-23°W	22-24	65
Madagascar	10°S-25°S	45°E-50°E	18-21	65
Mozambique	20°S-25°S	35°E-40°E	18-21	25
Nigeria	4°N-6°N	4°E-9°E	22-24	30
Rio Muni	2°N-3°N	10°E	20-22	30
Sao Tome and Principe	0°N-2°N	7°E-9°E	22	1-10
Senegal	13°N-17°N	16°W-17°W	18	50
Sierra Leone	7°N-9°N	12°W-14°W	20-22	100
Somalia	10°N-2°S	41°E-50°E	18-20	25
Togo	6°N	2°E-3°E	22-24	50
United Republic of Cameroon	3°N-4°N	9°E-10°E	22-24	65
United Republic of Tanzania	5°S-10°S	35°E-40°E	20-22	25
Zaire	5°S-6°S	12°E	20-22	50
Latin America				
Bahamas	25°N	77°W-79°W	20-22	15
Barbados	13°N	58°W-60°W	22	1-10
Belize	16°N-17°N	87°W-88°W	22	50
Brazil	4°N-32°S	35°W-55°W	20-24	75
Colombia	2°N-12°N	63°W-79°W	20-22	50
Costa Rica	8°N-12°N	83°W-85°W	21-22	50
Cuba	20°N-23°N	75°W-85°W	22-24	1
Dominica	15°N-16°N	61°W-62°W	22	1-10
Dominican Republic	18°N-20°N	68°W-72°W	21-24	1
Ecuador	2°N-4°S	79°W-81°W	18-20	50
El Salvador	13°N-14°N	87°W-90°W	22	65
French Guiana	4°N-5°N	50°W-52°W	22-24	130
Grenada	13°N	61°W-62°W	27	1-10
Guatemala	14°N-17°N	88°W-94°W	22	65
Guyana	5°N-8°N	58°W-60°W	22-24	130
Haiti	18°N-20°N	72°W-75°W	21-24	1
Honduras	14°N-16°N	83°W-88°W	22	65
Jamaica	18°N-19°N	76°W-78°W	22	1-10
Lesser Antilles	12°N-18°N	61°W-65°W	22-24	1
Mexico	17°N-22°N	104°W-108°W	20-22	32
Nicaragua	11°N-14°N	84°W-86°W	22	65
Panama	8°N-9°N	76°W-83°W	21-22	50
St. Lucia	13°N-14°N	61°W-62°W	22	1-10
St. Vincent and the Grenadines	13°N-14°N	61°W-62°W	22	1-10
Suriname	4°N-5°N	52°W-58°W	22-24	130
Trinidad and Tobago	11°N	61°W	22-24	10
Venezuela	8°N-12°W	60°W-73°W	22-24	50
U.S. Virgin Islands	18°N	65°W	21-24	1

Under its responsibilities of the OTEC Act of 1980, NOAA has issued regulations for licensing commercial OTEC plants (NOAA 1981b), an environmental impact statement on the licensing of commercial plants (NOAA 1981a), a technical guidance document on the environmental requirements of the regulations (NOAA 1981c), and a research plan for assessing environmental effects that may accompany the commercialization of OTEC (NOAA 1982).

ESTIMATED OPERATING CONDITIONS FOR INITIAL U.S. OTEC DEPLOYMENTS

This chapter presents preliminary estimates of site characteristics and operating conditions for early OTEC developments. Two areas are so characterized because of the interest for OTEC in these areas: The western coast of Oahu, Hawaii, in the vicinity of Kahe Point (Fig. 2); and the southeastern coast of Puerto Rico in the vicinity of Punta Tuna (Fig. 3). Both near/onshore and open-ocean sites near Oahu and Puerto Rico are considered in the following description which is primarily based on an evaluation of information presented by Bathen (1975, 1977, 1978), EG&G (1980), Miller (1977), Noda et al. (1980), Ocean Data Systems, Inc. (1977a,b), and Wolff (1978).

General Site Characteristics

Temperature, Salinity, and Density Profiles—In the vicinity of Kahe Point, Oahu, Hawaii, the probable surface temperature varies from 24.1°C in late winter to 26.9°C in midsummer. The likely range of surface temperatures is generally within 1.2°C of these probable values. At a depth of 700 m the probable temperature varies from 5.2 to 5.5°C. At a depth of 1000 m the temperature is about 4.2°C with very little variation. The thickness of the mixed layer typically varies from as little as 10 m to as much as 180 m; however, the probable thickness of the surface mixed layer varies from 40 to 100 m, being deepest during the winter and shallowest in the summer. The average nearsurface salinity is about 34.8 ppt and increases to about 35.1 ppt at the bottom of the surface waters (a depth of 100-125 m), and then decreases again to about 34.1 ppt at a depth of about 450 m. The density profile is dominated by temperature, but salinity variation has some effect due to the salinity maximum occurring near the thermocline (just below the bottom of the surface mixed layer).

In the vicinity of southeastern Puerto Rico the probable surface temperature varies from 26.2°C in winter to 29.2°C late summer and early fall. The likely range of surface temperatures is generally within ±2.3°C during spring and fall. At a depth of 700 m the probable temperature is 7.9-8.2°C. At a depth of 1000 m the temperature is about 5.3°C with very little variation. The thickness of the mixed layer typically varies from as little as 10 m to as much as 140 m; however, the probable thickness of the surface mixed layer varies from 40 to 100 m, being deeper during the winter and shallower in the summer. The nearsurface salinity is about 35-36 ppt and increases to a maximum of about 36.7 ppt at a depth of 100-125 m. The salinity minimum is about 35 ppt at a depth of 700-900 m.

Currents—The ocean currents near Kahe Point, Oahu, Hawaii, are fairly complex, being a combination of tidal (i.e., depth-averaged, shelf) currents, geostrophic (i.e., upper water column of deep water) flow, and wind-driven (i.e., surface) currents. The tidal current has both a semidiurnal and a diurnal component. The flood-tide is basically parallel to the shore, flowing in the south-southeast direction. The maximum semidiurnal component of the current is about 20-30 cm/s while the diurnal component is 10-20 cm/s. The geostrophic flow is highly variable and can exceed 60 cm/s in larger eddies, although near Kahe Point currents on the order of 15-25 cm/s are more typical. The magnitude of wind-driven currents (i.e., surface) depends on the wind strength, but values of 9-10 cm/s are typical. Wind-driven currents tend to be shore-parallel near Kahe Point.

The currents discussed above are highly variable in magnitude and direction. The mean flow near Kahe Point is difficult to determine but is estimated to be on the order of or less than 10 cm/s. In shallower areas nearshore, this flow tends to be more shore-parallel. The net flow of the surface waters in the vicinity of Hawaii tends to be westward, being part of the North Pacific Equatorial Current.

Ocean currents in the vicinity of southeastern Puerto Rico are generally westward flowing due to the South Atlantic Drift, which is driven by the North Atlantic Trades. The currents tend to follow the bathymetric contours (and thus tend to be shore-parallel) but are highly variable. The mean current is typically 10-40 cm/s in the deep offshore waters (< 1000 m deep) and slightly higher (60 cm/s) nearshore.

General Plant Characteristics

Type of Plant—The first OTEC plants are expected to be of the closed-cycle type using ammonia as the working fluid. Smaller plants (of the pilot-plant scale) will probably be located on or nearshore or on bottom-mounted towers in about 100 m of water. Larger plants (of commercial scale) will likely be either on bottom-mounted towers or offshore in the form of moored floating plants or free-floating plantships.

Plant Capacity—OTEC plants are expected to be made up of multiple units which can operate independently. A typical pilot plant might be made up of four to six 10-MWe units, while eventually ten to twenty 25-MWe units might be typical for commercial plants (W. H. Avery, Director, Ocean Energy Programs, Johns Hopkins Univ. Appl. Physics Lab., Laurel, MD, pers. commun. 1984).

Plant Dimensions—Pilot plants located on or nearshore where space is not particularly limited will have horizontal dimensions on the order of 100 m. Bottom-mounted plants (on towers) will make use of the space along the vertical extent of the tower and thus will have horizontal dimensions on the order of 50 m. Larger plants (commercial scale) in the open ocean are expected to be 100-150 m in diameter for cylindrically symmetric designs and 50-75 m wide × 150-200 m long for ship or barge type designs.

Power System

Working Fluids—Most designs for first-generation OTEC plants specify ammonia as the working fluid. Other fluids that have been considered are noted in Table 2.

Heat Exchangers—Initially heat exchangers will be of aluminum or titanium but eventually other materials may be used. Designs

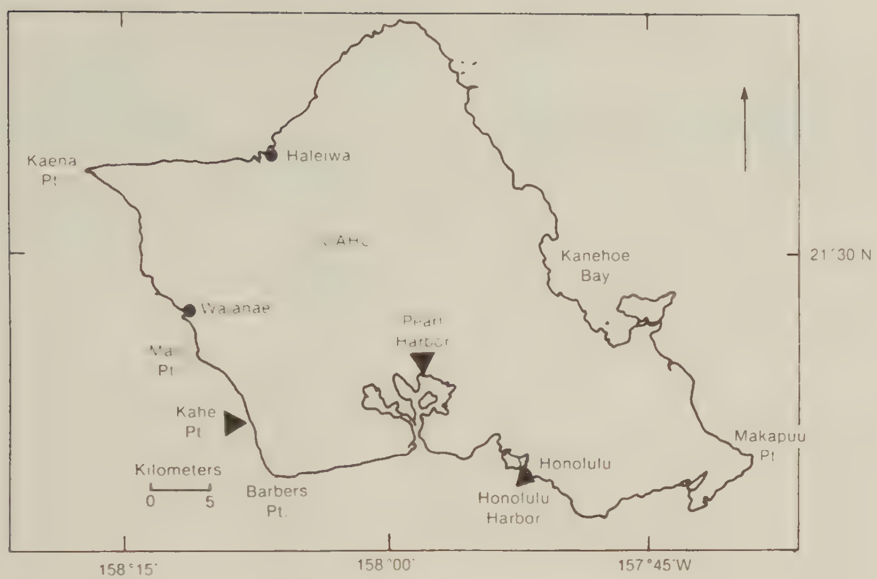
Kaena Pt
Haleiwa
OAHU
Kanehoe Bay
21°30' N
Waianae
Pearl Harbor
Ma Pt
Kahe Pt
Makapuu Pt
Honolulu
Kilometers
0 5
Barbers Pt.
Honolulu Harbor
158°15'
158°00'
157°45'W

Figure 2.—The Kahe Point area, Oahu, Hawaii.

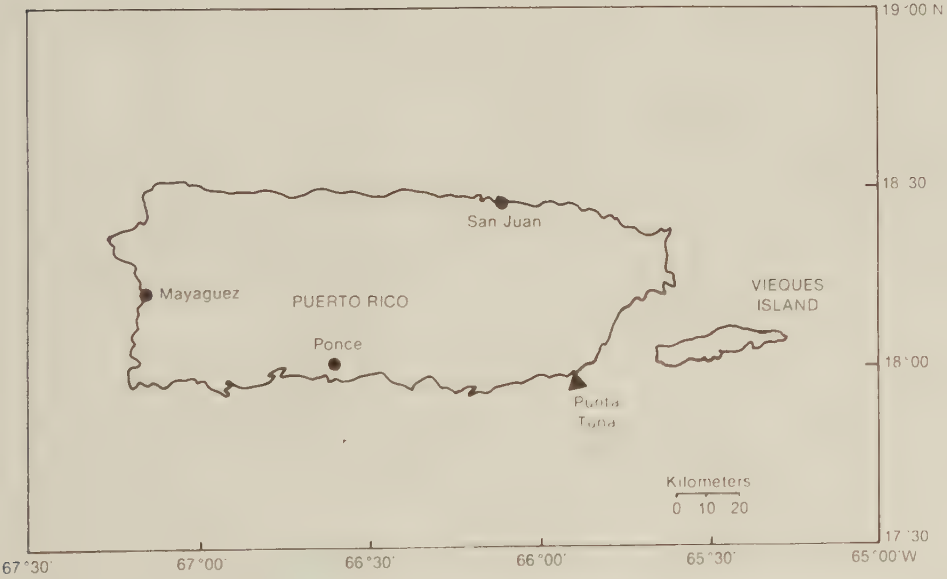
19°00' N
18°30'
San Juan
VIEQUES ISLAND
Mayaguez
PUERTO RICO
Ponce
18°00'
Punta Tuna
Kilometers
0 10 20
17°30'
67°30'
67°00'
66°30'
66°00'
65°30'
65°00'W

Figure 3.—The Punta Tuna area, Puerto Rico.

Table 2.—Characteristics of some candidate OTEC working fluids.

Fluid	Physical state*† (20°C)	Clean Water Act (1977) standing	Water solubility*† (in 100 ml H_2O)	Flammability**	Explosion hazard**	Disaster hazard	OSHA[c] 8-h exposure limits†† (ppm)	Human toxicity**,[d]	Carcinogenicity**
Ammonia	Gas	Hazardous substance	90 g (0°C)	671°C[a]	Moderate (when exposed to flame)	Moderately dangerous (emits toxic fumes when exposed to heat)	50	High	None
Freon™ 22	Gas	Not regulated	Insoluble	632°C[a]	No data	Dangerous (emits highly toxic fumes when heated to decomposition or on contact with acid or acrid fumes) Atmospheric release may contribute to potential degradation of the ozone layer.	No data	Low	None
Freon™ 11	Liquid	Not regulated	Insoluble	No data	Reacts violently with molten aluminum	Dangerous (emits highly toxic fumes of fluorides and chlorides when heated to decomposition) Atmospheric release may contribute to potential degradation of the ozone layer.	No data	Low	None
Methyl chloride	Gas	Toxic pollutant	400 g	632°C[a] <0°C[b]	Moderate (Reacts violently with aluminum)	Dangerous (emits highly toxic fumes when heated to decomposition; reacts vigorously with oxidizing materials)	100	Moderate	None
Methylene chloride	Liquid	Toxic pollutant	2 g (20°C)	615°C[a]	None under ordinary conditions	Dangerous (emits highly toxic fumes when heated to decomposition)	500	Moderate	None
Nitrogen dioxide	Gas	Hazardous substance	7 g (0°C)	No data	Reacts violently with aluminum	Dangerous (emits highly toxic fumes when heated to decomposition, reacts with water or steam to produce heat and corrosive fumes)	5	High	None
Methyl formate	Liquid	Not regulated	30 g (20°C)	465°C[a] −2°C[b]	Moderate (when exposed to heat or flame)	Dangerous (emits toxic fumes when exposed to heat or flame; reacts vigorously with oxidizing materials)	100	Moderate	None
Methyl amine	Gas	Not regulated	807 g (12°C)	430°C[a] 0°C[b]	Moderate (when exposed to spark or flame)	Dangerous (reacts vigorously with oxidizing materials)	10	Moderate	None
Ethyl amine	Liquid	Not regulated	Soluble	385°C[a] <−17°C[b]	No data	Dangerous (reacts vigorously with oxidizing materials)	10	High	None

[a] Autoignition temperature

[b] Flash point

[c] Occupational Safety and Health Administration

[d] Low - causes readily reversible tissue changes which disappear after exposure ceases.
Moderate - may cause reversible or irreversible changes to exposed tissue, no permanent injury or death.
High - capable of causing death or permanent injury in normal use; poisonous.

SOURCES:
* P. Holtzclaw, U.S. EPA, 401 M St. SW, Wash., D.C., pers. commun. 1981.
† Hodgman, 1959
** Sax, 1979
†† United States Department of Labor, 1972

suitable for OTEC applications involving tube-in-shell, plate types, and folded tube heat exchangers have been successfully tested at small scale under OTEC conditions (Avery, pers. commun. 1984).

Biofouling Control—Most designs will use periodic (daily) chlorination for biofouling control. Some designs also plan to use mechanical cleaning methods, such as Amertap™ balls or M.A.N.™ brushes, in conjunction with chlorination. The dose of chlorine needed to prevent biofouling will be somewhat dependent on site-specific characteristics; however, recent studies suggest doses on the order of 0.07 mg/L (70 ppb) injected 1 hour/day may be sufficient (Larsen-Basse and Daniel 1983).

Operating Efficiencies—Overall thermal operating efficiencies for most OTEC plants are expected to be in the 2-3% range. However, certain pilot-plant designs use larger than normal warm-water flow rates to take advantage of less expensive heat exchangers. Such designs will have efficiencies in the 1.0-1.5% range.

The thermal efficiency is the fraction (usually expressed as a percent) of the heat energy extracted from the warm water that is converted into net electrical energy. For normal OTEC operating temperatures, this efficiency is limited to 6.0-7.5% by the basic laws of thermodynamics. Therefore, a more useful quantity might be the "effectiveness" of the plant which is the ratio of the net electrical power available for external use to the gross power produced by the turbo-generator system. This ratio is 65 to 75% for typical designs (increases rapidly with delta-T) and may fall to 35% for shore-based sites where the needed cold-water pipe lengths require higher pumping power (Avery, pers. commun. 1984).

Seawater Systems

Warm Water Intake

Depth and location—The warm-water intake will be located in the upper part of the surface mixed layer of the ocean to take advantage of the warmest water available. Intakes for pilot plants will be about 10 m deep, while intakes for larger commercial plants will have to be about 20 m deep due to the larger intake flow-rate requirements.

Shape and orientation—The intake structure will generally be constructed to produce horizontal flows external to the structure because it appears that fish can sense and avoid horizontal flows better than vertical flows (see Impingement section). The structure will also be much larger in the horizontal direction than in the vertical direction to keep intake velocities low and yet keep the structure near-surface where the warmest water is located.

Flow rates and intake velocities—Typical warm-water flow rates for OTEC designs are in the range of 3-5 $m^3 \cdot s^{-1} \cdot MWe^{-1}$. However, flow rates as high as 8.5 $m^3 \cdot s^{-1} \cdot MWe^{-1}$ are proposed for plants intending to trade larger flow rates for less expensive heat exchangers. Flow velocities in the warm-water pipes and conduits will generally be in the 1.5-2.5 m/s range, but intakes are expected to be designed to reduce the velocity to 0.25-0.30 m/s outside the intake structure. The low intake velocities can lead to rather large intake area requirements for large (100-MWe) plants.

Cold Water Intake

Depth and location—The cold-water intake for most OTEC designs will be at the end of a long pipe extending to a depth of 750-1000 m. The selection of the depth at which the cold water will be withdrawn is the result of a trade-off between the efficiency gained by colder temperatures and the added expense of constructing and operating a longer cold-water pipe.

Shape and orientation—Because the cold-water intake will be located in an area of low biological activity, little effort has gone into design of the intake structure; most likely, it will be an open-ended pipe with bar screens placed to keep out relatively large objects.

Flow rates and intake velocity—Typical OTEC designs call for cold-water flow rates comparable to the warm-water flow rate, in the range of 3-5 $m^3 \cdot s^{-1} \cdot MWe^{-1}$. However, some designs try to reduce the cold-water requirements because of the expense of obtaining water from such depths. Flow velocities in the cold-water pipe will generally be in the 1.5-2.5 m/s range. Intake velocities may be of this same order because it is generally thought that there is no need to reduce the intake velocity at the great depths involved. However, lower intake velocities can be achieved, if needed, by use of a flared pipe section. Ocean Thermal Corporation will use such a section to reduce the cold-water intake speed to 0.3 m/s for the Kahe Point design.

Discharge

Depth and location—Most OTEC designs will try to locate the discharge so as to reduce the potential for recirculation of effluent into the warm-water intake. Although this may be accomplished through either separate or mixed effluent discharges, most designs depend on the density of the effluent being greater than the density within the mixed layer so that the effluent will come to equilibrium near the bottom of the mixed layer, out of the influence of the intake. For nearshore plants this may involve the use of a discharge pipe leading offshore. In deeper waters it is anticipated that the discharge will generally be located at a depth of 30 m or greater to avoid recirculation.

It is expected that the temperature of the warm water and cold water will decrease about 2-3°C during passage through the heat exchangers. For representative warm and cold waters of 25°C and 5°C, respectively, temperatures of separate warm and cold discharges would then be about 22-23°C and 7-8°C, respectively. For this situation, a mixed discharge would have a temperature near 15°C.

Shape and orientation—Most proposed designs do not involve the use of any special discharge structures such as multiport diffusers (see Effluent Discharge section). Thus, the discharges will be from open-ended round pipes directed either downward or horizontally (often with a downward component).

Flow rates and discharge velocity—Discharge flow rates must equal intake flow rates due to continuity. Typically, discharge velocities will be in the 1.5-2.5 m/s range.

PHYSICAL INTERACTION WITH THE ENVIRONMENT

The presence of an OTEC plant will cause a physical interaction with the marine environment. However, with the exception of some small modification of water movement in the immediate vicinity of a plant, the principal physical interaction will be due to the intake and discharge of the relatively large volumes of water needed for an OTEC operation. These topics are discussed in this section since they are so important to the definition of biological interaction taken up in the later section on Biological Interaction.

Cold Water Intake

The cold water intake provides the cold water needed for the condensing part of the OTEC cycle. Given a certain surface temperature, a cold water pipe (CWP) will have to be extended deep enough to obtain cold water at a temperature low enough to assure a temperature difference (ΔT) of about 20°C. Certain engineering constraints will be present, however, in obtaining the cold water, e.g., the large pipe diameters and depths required for bottom-mounted pipe installations both exceed the demonstrated capability of the offshore pipe laying industry (Brewer 1979). However, it is believed that these problems may be overcome with a minimum extension of present technology. The CWP may either be

1. emplaced on a shelf, extending to the needed depth for a land-based OTEC plant;
2. placed vertically within the structure of a shelf-sitting tower to the needed depth, or to the seabed and then extended on the shelf to the needed depth; or
3. placed vertically to the required depth beneath an open ocean plantship.

To obtain a ΔT of about 20°C, the CWP intake will need to be located at a depth of about 800-1000 m in most locations. At this depth the induced flow will not interact with other intake and discharge flow fields, and the interaction with the environment will depend primarily on the volumetric flow rate (Paddock and Ditmars 1983). Therefore, the intake depth, volumetric withdrawal rate, and velocity are the three principal variables that will define the interaction.

Warm Water Intake

Like the need for cold water, a relatively large volumetric rate of warm water is needed for the evaporation part of the OTEC cycle (see section on Flow Rates and Intake Velocities).

In general, the warm water intake will draw water from a range of depths, dependent upon the ambient density stratification in the vicinity of the intake, the flow rate at which water is withdrawn, and the size and shape of the intake structure (Paddock and Ditmars 1983). The volumetric flow rate at which water will be withdrawn will depend, among other factors, on thermodynamic needs of the power cycle and the efficiencies of the heat exchangers. Once the volumetric flow rate is established, however, a trade-off is involved between the intake dimension and the velocity of the flow—the less the intake dimensions, the greater the intake velocity and vice versa. For example, consider the intake of 140 m^3/s of warm water for a 40-MWe OTEC plant (i.e., 3.5 $m^3 \cdot s^{-1} \cdot MWe^{-1}$). Using an intake pipe of 34 m diameter would result in an intake velocity of 15 cm/s, whereas an intake pipe of 17 m would impart an intake velocity of 62 cm/s. Using an intake pipe of 10 m diameter would result in an intake velocity of 178 cm/s for which the power loss due to friction would be small, whereas an intake diameter of 5 m would entail a velocity of 713 cm/s which would cause an unacceptable friction loss (Avery, pers. commun. 1984).

The effect of the warm water intake on the flow field in the vicinity of the intake structure will also be dependent upon a number of factors. To provide an idea of the possibilities, three induced flow patterns are indicated in Figure 4 for three simplified hypothetical intake situations:

1. Intake flow field in the presence of an ambient current for an intake distributed uniformly over the mixed layer where the density is constant above and below a strong thermocline (Fig. 4a);
2. intake flow field in the presence of an ambient current for a point intake within the mixed layer, again where the density is constant above and below the thermocline (Fig. 4b); and
3. intake flow field for a point intake in a stagnant, linearly stratified environment (Fig. 4c).

These hypothetical scenarios provide an indication of the variety of cases that will determine where seawater and organisms are withdrawn. The quantification of the pertinent variables for such cases has been discussed by Paddock and Ditmars (1983).

Most ocean environments exhibit some variations of seawater density with depth (i.e., density stratification) such as shown in Figures 5 and 6 for Kahe Point and Punta Tuna, respectively. In the case of intake withdrawal from a density-stratified environment, selective withdrawal occurs. Selective withdrawal involves the flow of water from discrete layers centered about the elevation of the intake as shown in Figure 4c. The thickness of the layer withdrawn (σ) is inversely proportional to the degree of stratification, so that thinner layers will be withdrawn when strong stratification is present.

Effluent Discharge

The discharge of used warm and cold OTEC waters may be either separate or mixed. Additionally, a discharge could be through a single discharge pipe, through a number of discharge pipes if the dimensions of a single discharge structure became unrealistic, or through a multiple port diffuser. Multiple port diffusers are commonly used for the discharge of municipal waste to ocean waters (Koh 1983) and have been considered in hydraulic studies of OTEC discharges. Although multiple port diffusers could ensure a greater degree of dilution of an OTEC effluent, it is not obvious that this is the desired objective, as discussed below. Furthermore, problems with construction, head losses, and additional pump requirements might outweigh possible advantages of a multiple port diffuser, to say nothing of additional biological concerns over the greater volume of dilution water needed.

A separate discharge scheme would involve separate discharges for both the warm and cold waters, whereas a mixed discharge scheme would utilize the same discharge structure for both water types. Although the initial physical fates of the discharged water would vary according to the scheme employed, the physics that define these fates are the same for both cases and relate to the behavior of buoyant discharges.

The behavior of positively or negatively buoyant discharges has been studied analytically as well as through the use of physical models. Initially these studies were conducted to evaluate the behavior of cooling water discharges from conventional power plants and of effluents from sewage outfalls; recently such studies have

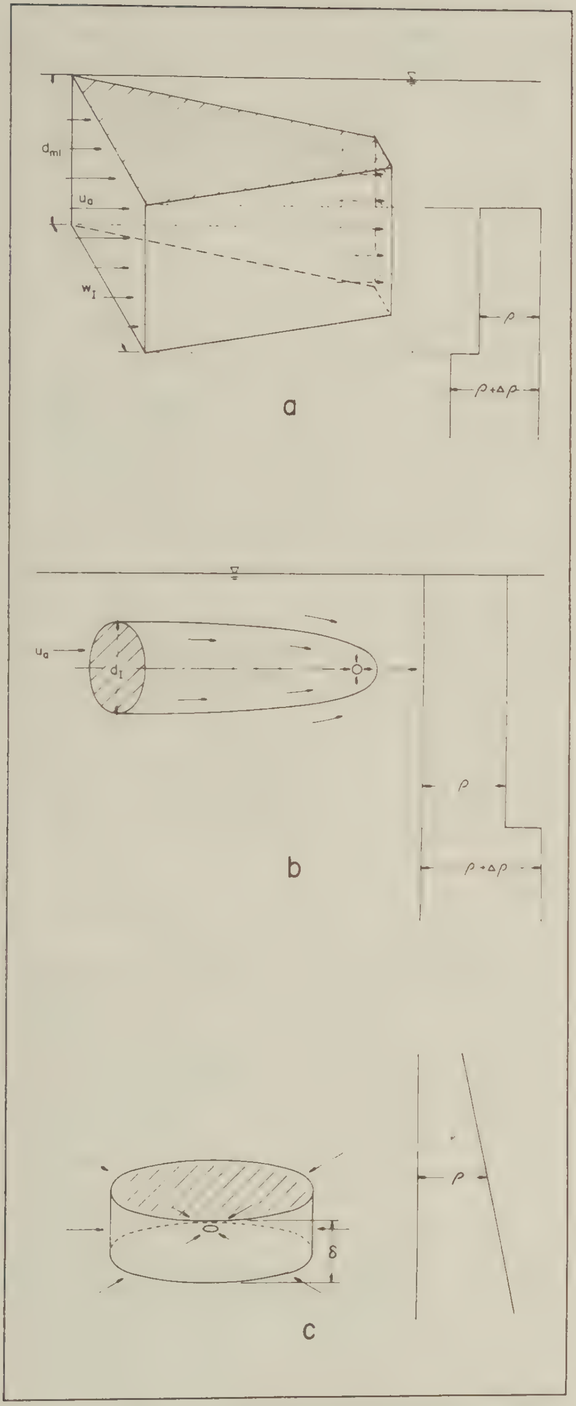

Figure 4.—a. Schematic of the intake flow field in the presence of an ambient current for an intake distributed uniformly over the mixed layer (from Paddock and Ditmars 1983). b. Schematic of the intake flow field in the presence of an ambient current for a point intake within the mixed layer (from Paddock and Ditmars 1983). c. Schematic of the intake flow field for a point intake in a stagnant, linearly-stratified environment (from Paddock and Ditmars 1983).

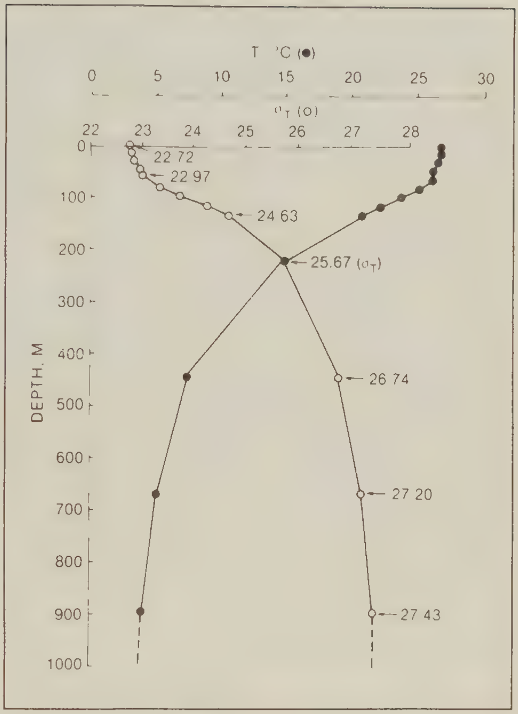

Figure 5.—One temperature and density profile offshore Kahe Point, Oahu, Hawaii (from Noda et al. 1981a; site 1, cast 1, 6 November 1980).

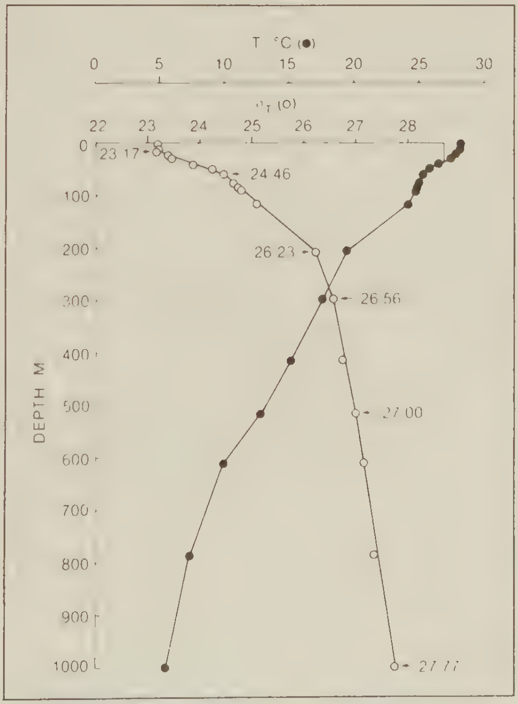

Figure 6.—One temperature and density profile offshore Punta Tuna, Puerto Rico (from Vargo et al. 1981; daycast, PROTEC-13).

been applied to OTEC discharges (Allender et al. 1978; Ditmars 1979; Ditmars and Paddock 1979). Although details of such assessments may be quite complex and dependent upon site-specific factors, generalities can be made for certain simplified situations (Paddock and Ditmars 1983). As discussed by Paddock and Ditmars, different phenomena govern the different regions of the flow that develop, termed the near-field, intermediate-field, and far-field (Figs. 7, 8). Momentum and buoyancy dominate in the near-field, gravity and interfacial shear in the intermediate field, and advective and dispersive mechanisms in the far field.

The important parameters about the near-field region are primarily the depth where the discharge plume reaches neutral buoyancy (equilibrium depth), the average dilution achieved by the discharge plume upon reaching the equilibrium depth (initial dilution), and the trajectory from the point of discharge to the equilibrium depth. Paddock and Ditmars (1983) present methods for quickly estimating these parameters for simplified situations. As an example, consider the discharge from 40-MWe hypothetical OTEC plants located offshore of (1) Kahe Point, Oahu, Hawaii, and (2) Punta Tuna, Puerto Rico. The plants pump 140 m^3/s of both cold and warm water for a total flow and discharge of 280 m^3/s. Four cases are considered to give an indication of the range of behavior that might be expected:

1. Separate horizontal round discharges to nearsurface waters (20 m);
2. separate horizontal round discharges at depth (100 m);
3. mixed horizontal round discharge to nearsurface waters (20 m); and
4. mixed horizontal round discharge at depth (100 m).

For all four cases, it is assumed that stagnant conditions prevail, the density profiles of Figures 5 and 6 apply, and the intake waters are from 20 m and 1000 m with the following ambient properties:

	Temp. (°C)	Salinity (ppt)	σ_t
Kahe Point			
Warm Water	26.6	34.9	22.8
Cold Water	3.8	34.5	27.4
Punta Tuna			
Warm water	27.7	36.0	23.3
Cold Water	5.4	35.2	27.8

It is also assumed that the warm water will undergo a temperature drop of 2°C and that the cold water will undergo a temperature increase of 2°C. Based on tables of seawater density in Fischer et al. (1979), these temperature changes would produce sigma-t's (σ_t) of approximately 23.4 for the warm water side and 27.2 for the cold water side at Kahe Point, and 23.9 for the warm water side and 27.5 for the cold water side at Punta Tuna. All discharges are made through 10-m diameter pipes, whether separate or mixed. For the case of mixed discharges, the discharge velocity is kept constant at 1.8 m/s by using two 10-m diameter pipes. It is assumed that the discharges do not interfere with each other. Using the approximation methods of Paddock and Ditmars (1983) leads to the following results.

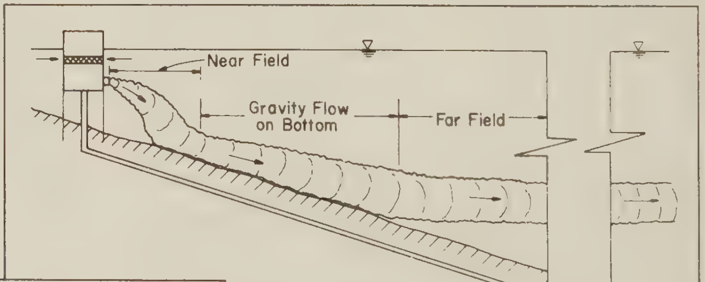

Figure 8.—Typical discharge flow field for an OTEC plant located in shallow water showing flow along the bottom (from Paddock and Ditmars 1983).

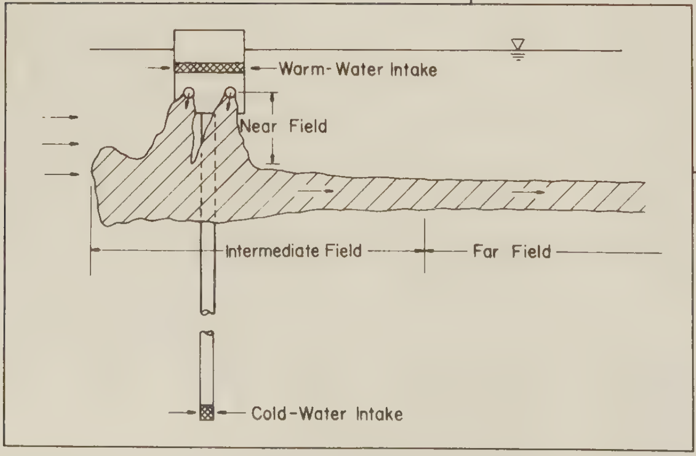

Figure 7.—Typical discharge flow field for an OTEC plant located in deep water (from Paddock and Ditmars 1983).

	Discharge	Level of neutral buoyancy, m	Dilution
Kahe Point			
Separate to nearsurface (20 m)	Warm	50	6.5
	Cold	80	7
Separate to depth (100 m)	Warm	95	4
	Cold	145	6
Mixed to nearsurface (20 m)	Mixed	75	6.5
Mixed at depth (100 m)	Mixed	120	4.5
Punta Tuna:			
Separate to nearsurface (20 m)	Warm	30	4
	Cold	55	5.5
Separate to depth (100 m)	Warm	75	5
	Cold	160	7
Mixed to nearsurface (20 m)	Mixed	45	4.5
Mixed at depth (100 m)	Mixed	115	5

Although the above results are only rough approximations, they provide insights that are useful for defining physical interaction with the environment. In general, it can be seen that initial dilution for OTEC discharges will be in the range of about 1 to 10. The strong effect of density stratification is also apparent and suggests that wherever an OTEC discharge plume encounters a strong density gradient, its further vertical motion will be limited. Not only do strong density gradients arrest a plume's trajectory, they also limit the amount of dilution that can be achieved. The presence of currents would act to lengthen the trajectory of the discharge plume and increase the dilution achieved; accordingly, the depth of neutral buoyancy of an effluent plume might be somewhat less for a negatively buoyant discharge.

Regional Influence

Using approximation methods discussed by Paddock and Ditmars (1983), it can be shown that the above initial dilutions and levels of neutral buoyancy will occur in a time frame on the order of a minute. Referring back to Figures 7 and 8, it can then be inferred that the intermediate and far field processes will have a greater influence on regional environmental impacts. Examining a hypothetical 40-MWe OTEC plant in typical tropical ocean conditions, Jirka et al. (1980) analyzed the spreading of a mixed discharge plume in a density stratified environment. The results indicated the effluent plume to be about 10 m thick and 5 km wide. This size is comparable with island shelf areas and warrants an analysis of the regional environmental influence of even a small OTEC plant.

Aware that the regional influence of an OTEC operation could be considerable, NOAA initiated a research effort in 1982 with Argonne National Laboratory to develop a model that could define this influence. To come to an understanding of the influence, a description was needed of the physical processes associated with the discharge of large volumes of water into the upper ocean by OTEC plant operations. The approach taken departed from previous mathematical modeling investigations of OTEC plant interactions with the ocean environment. In previous modeling, effluent plumes and intake flows have been superimposed on fixed ambient ocean waters; that is, no attempt was made to model changes in the ocean resulting from their presence. The Argonne model simulates the interaction of an OTEC discharge with the ocean, thereby permitting discharge-induced modifications to the ambient ocean to be determined. Changes in ambient circulation, temperature structure, and concentration of effluent and water column constituents are modeled. The general approach was to modify an existing three-dimensional model for limited-area coastal regions (Wang 1982) by incorporating simulations of the effluent flows due to an OTEC operation. The effect of the intake flow was found to be minimal and thus is not included in the model.

The Argonne model was applied to a base case of a 280 m^3/s mixed discharge from a 40-MWe OTEC plant into coastal waters for various ambient ocean conditions, and then was used to examine the effect of two nearby 40-MWe plants and that of an 80-MWe plant. Applied to the case of a mixed discharge from a 40-MWe OTEC plant located in deep water on a coastal margin, the Argonne model indicated the effluent plume will be confined mostly to the top of the thermocline. In the case of an ambient alongshore current of 20 cm/s, the addition of a conservative dye to the discharge indicated the effluent plume to be about 20 m thick, 2 km wide, and 4 km long (Fig. 9), and diluted by a factor of 20-100. Because the plume is mainly driven by the buoyant discharge, the regional influence does not depend on the details of the mode of discharge (e.g., single or multiple outlet discharge). Temperature perturbations are caused by the dilution of the effluent and by the redistribution of ambient temperature structure. For a 40-MWe OTEC plant discharge, temperature perturbations are less than 0.2°C and are distributed almost uniformly between the bottom of the mixed layer and the top of the thermocline.

The circulation induced by interaction of the buoyant discharge and the ocean not only influences plume dilution and temperature structure but also contributes to the redistribution of other ocean constituents. A computation of a nitrate profile subjected to only the physical (conservative) aspects of OTEC operation indicated that the nitrate flux into the upper ocean is derived both from the mixed-discharge effluent (i.e., cold water influence) and from discharge-induced deep upwelling. For a base condition where the nitrate level is very little in the upper 90 m and increases to some higher level in the depth interval of 90-130 m, the two processes contribute about equal amounts of the OTEC-induced nitrate flux into the upper ocean.

Using the Argonne model to examine the effects of discharges of two adjacent OTEC plants showed that the regional influence may be computed as a superposition of two individual plumes, given reasonable separation between plants. When two 40-MWe OTEC plants are separated by 2 km alongshore, the effluent concentration near the up-current plant is about the same as the effluent concentration of a 40-MWe OTEC single plant, where the effluent concentration near the down-current plant is increased by about 25% (Fig. 10). When two plants are separated by only a few hundred meters, which is equivalent to the case of a single 80-MWe OTEC plant, significant interaction occurs and the effluent concentration is increased by about 100% from that of a single 40-MWe OTEC plant.

The regional influence is not very sensitive to the effects of the coastal boundary. On the other hand, the dilution of the effluent plume is greatly reduced for effluents discharged in shallow water or along the bottom. For a 40-MWe OTEC plant with bottom discharge, the maximum effluent concentration will be about 10% of the initial concentration, which is about twice the maximum concentration of the effluent plume from the nearsurface discharge. The plume also penetrates deeper into the thermocline than in the case of nearsurface discharge.

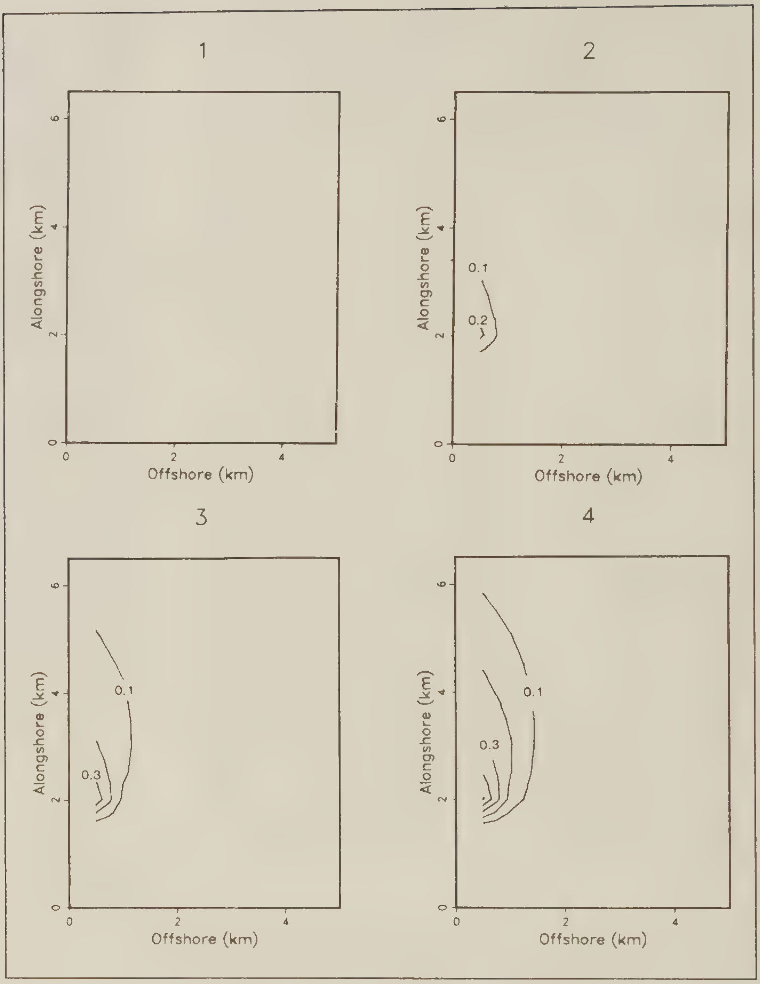

Figure 9.—Horizontal distribution of dye at 10 m (level 1), 30 m (level 2), 50 m (level 3), and 70 m (level 4) from a model of the regional influence of a 40-MWe OTEC plant (initial concentration = 10; ambient current = 20 cm/s alongshore) (from Wang 1984).

The applications of the Argonne model to several OTEC configurations have demonstrated the importance of the discharged-induced circulation, or interactions between the discharge and ambient ocean. The region of influence of an OTEC facility clearly is greater than simply the geometric extent of the plume determined from integral jet models and superimposed on a fixed ambient ocean. For the purpose of investigating regional influence in a generic sense, model applications have been restricted to a simple coastal geometry and steady ocean currents. In the case of a more complex geometry, the effluents that are advected downcurrent may accumulate in a convergence zone. The effluent plume also may be swept away by storm currents and impinging eddies.

BIOLOGICAL INTERACTION WITH THE ENVIRONMENT

Biological Characteristics of the Environment

This section briefly summarizes information presented in reports by Hoss et al. (1983) and Uchida (1983) (both efforts being part of this overall study), on pertinent biological information from the Caribbean and Pacific, respectively. For specific details those reports should be directly consulted.

Location—There are no areas in the Caribbean which lie outside of existing or potential Exclusive Economic Zone claims of some nation. It is likely that OTEC operations by U.S. corporations will be within the Fishery Conservation Zone (equivalent to the Exclusive Economic Zone in the U.S.) surrounding Puerto Rico and the U.S. Virgin Islands (Fig. 11). Several sites in the Pacific have been studied for possible land-based OTEC plants including Keahole Point and Kahe Point in the Hawaiian Islands and Cabras Island, Guam. Additional areas in the open Pacific (e.g., between lat. 5°-10°N and long. 90°-95°W) have been investigated and found to be excellent for OTEC plantship operation.

Phytoplankton—Primary production in Hawaiian and open tropical Pacific waters is low relative to that of Continental Shelf areas in the Pacific (estimated to be on the order of 200 g $C \cdot m^{-2} \cdot y^{-1}$) (Platt and Rao 1975). Noda et al. (1982) estimated the annual primary production off Keahole Point to range from 4.2 to 72.6 g $C \cdot m^{-2} \cdot y^{-1}$; measurements off Kahe Point are similar, with Noda et al. (1981a) determining average annual primary produc-

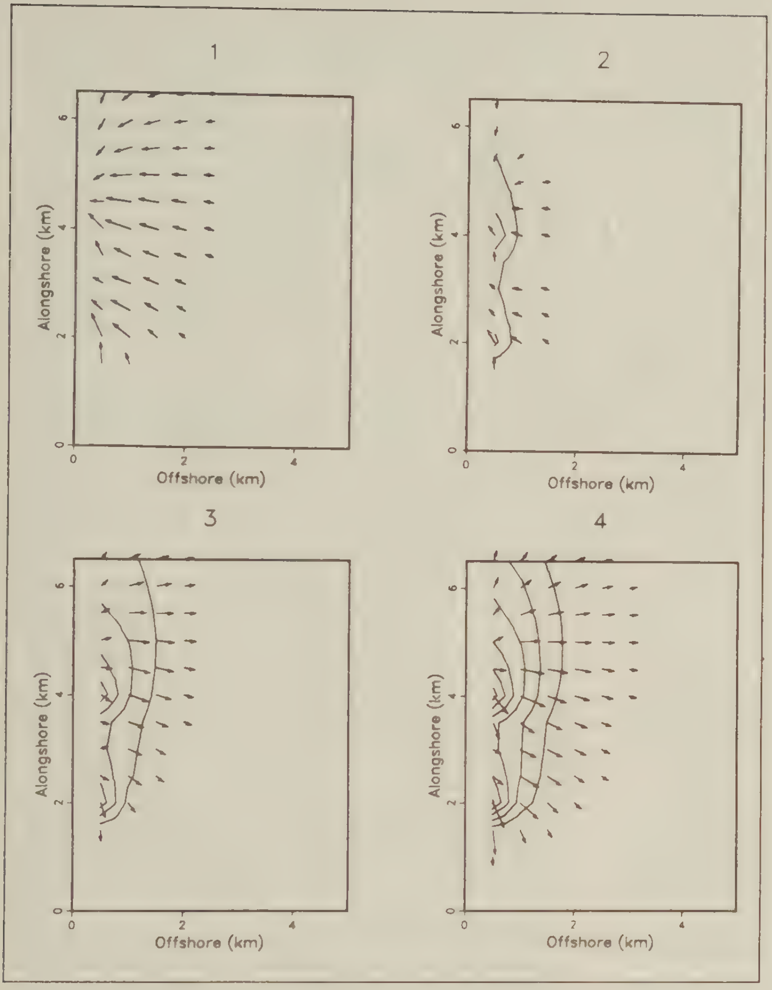

Figure 10.—Horizontal distribution of velocity and dye for two adjacent 40-MWe OTEC plants at 10 m (level 1), 30 m (level 2), 50 m (level 3), and 70 m (level 4) (velocity scale = 20 cm/s alongshore; initial dye concentration = 10; contour interval = 0.1) (from Wang 1984).

tion at 60.4 ± 15.6 g $C \cdot m^{-2} \cdot y^{-1}$. Slightly higher values, 120 to 144 g $C \cdot m^{-2} \cdot y^{-1}$, have been reported from the open ocean (El-Sayed and Taguchi 1979). Bienfang and Szyper (1982) demonstrated that enriching the photic zone with upwelled nutrients can increase production.

Production in the Caribbean is also generally low, typical of areas without a pronounced admixture of nutrient-rich water from below. Average daily production rates reported from various areas (Sander and Steven 1973; Steven 1971; Beers et al. 1968; and Steeman Nielsen and Jensen 1957) correspond to annual rates ranging from 20 to 105 g $C \cdot m^{-2} \cdot y^{-1}$. The variation is associated with input of nutrients to the surface: where water passes over shallow banks, at the edge of eddies which form in the wake of islands, at upwellings along the South American coast, and in upwellings on the periphery of eddies of Amazon river water. Potential OTEC sites near Puerto Rico and the U.S. Virgin Islands may be particularly low in primary and secondary production due to the thick wedge of low-density surface water present which may reduce nutrient advection.

Phytoplankton standing crop is similar at oceanic sites in the Caribbean, Hawaii, and the mid-Pacific. Surface chlorophyll-*a* concentration from eight Caribbean locations (Marshall and Solder 1982; Knauer and Flegal 1981; Sander and Steven 1973; Malone 1971; and Hargraves et al. 1970) averaged 0.13 mg m^{-3}. Off Keahole Point in Hawaii it ranged from 0.03 to 0.18 mg m^{-3} (Noda et al. 1982) and in the open tropical Pacific the average value was 0.12 mg/m^3 (El-Sayed and Taguchi 1979).

Investigations of plankton near oceanic islands have repeatedly revealed that taxonomic composition, standing crop, and production change with distance from shore. The intensity of this "island mass" effect and the area influenced are generally greater on the leeward side of the island. Data from Barbados (Sander and Steven 1973) showed that moving from 2 to 10 km offshore reduced cell concentration and production rates by a factor of four and increased the relative abundance of blue-green algae by a factor of ten. Because the intensity of this island mass effect varies with location, site-specific studies are particularly important at potential sites which are nearshore.

Zooplankton—Although zooplankton have not been studied extensively in either Hawaii or the Caribbean, the data available indicate similar abundance in both areas. In dry weights per sample from the Caribbean oceanic water, the range (0.3 to 12 mg/m^3) is similar to that found in Hawaiian nearshore samples, 0.14 to 25

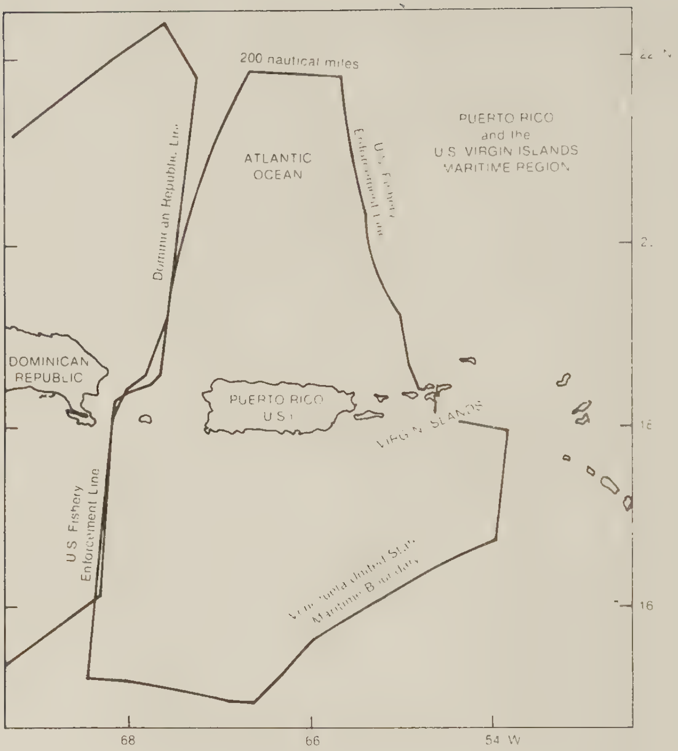
200 nautical miles
ATLANTIC OCEAN
PUERTO RICO and the U.S. VIRGIN ISLANDS MARITIME REGION
Dominican Republic Line
U.S. Fishery Enforcement Line
DOMINICAN REPUBLIC
PUERTO RICO U.S.
VIRGIN ISLANDS
U.S. Fishery Enforcement Line
Venezuela-United States Maritime Boundary
22 N
20
18
16
68
66
54 W

Figure 11.—The Fishery Conservation Zone surrounding Puerto Rico and the U.S. Virgin Islands (U.S. Department of State 1982).

mg/m^2 (Noda et al. 1981a). The average displacement volume, 0.20 to 0.30 ml/m^3, and average dry weight, 2.4-3.3 mg/m^3, are very similar among oceanic studies from the Caribbean (Moore and Sander 1977; Deevey 1971; Margalef 1971; and Moore 1967). The importance of an island effect on zooplankton abundance is evident from studies near Jamaica and Barbados where respective dry weights inshore were 1.7 and 2.5 times those found offshore (Sander and Steven 1973; Moore 1967).

Abundance of zooplankton decreases considerably with depth. Off Bermuda, total abundance in the upper 500 m was 8, 19, and 39 times that found at respective depths of 500-1000 m, 1000-1500 m, and 1500-2000 m (Deevey and Brooks 1971). In the mid-Pacific, Hirota (1977) showed the highest concentration in the upper 150 m and moderately high concentration between 200 and 900 m. Standing stocks in the upper 200 m varied about 50-90% of that in the upper 1000 m. Off of Kahe Point in Hawaii, Noda et al. (1981a) observed an approximate tenfold difference between surface samples and those from 600-1000 m.

Although diel migration of zooplankton has been observed but not extensively documented in Hawaii and the Caribbean, the phenomenon is general and fairly well known. "Diel vertical movements occur in all planktonic phyla and in most of the smaller taxonomic groups" (Longhurst 1976). In general this consists of a migration from deep water toward nearsurface layers, where plankton spend the night and then descend again at dawn. The plankters do not necessarily rise all the way to the surface; aggregations tend to occur at the level of the deep chlorophyll maximum, and abundance in the surface water may even decrease during the night as a result of downward migration of surface zooplankters to the chlorophyll maximum layer.

Fisheries—The major thrust of the commercial fishery in Hawaii is in the open ocean beyond 200 m in depth, where pole-and-line sampans catch skipjack tuna; and longline, handline, and charter boats harvest yellowfin and bigeye tuna, albacore, striped blue and black marlin, swordfish, spearfish, sailfish, wahoo, and mahimahi. Nearshore fisheries include a variety of commercial handline, net, trap, and recreational boats which catch a wide variety of demersal and bathypelagic species including pink, red, and grey snappers, goatfishes, seabass, and bigeye and mackeral scad. The scad landings are of considerable importance, being second only to tuna and billfishes.

The area near Kahe Point sustains a varied and valuable fishery. In the years from 1976 to 1980, 101 different species were identified in the harvest from the area. Hawaii Division of Aquatic Resources records show that the average annual catch was about 219 metric tons with an annual yield to commercial fishermen of $350,000.

The commercial fishery in the oceanic waters of the Caribbean is basically a long-line fishery for tunas. The fishery is dominated by large modern vessels from Japan, Korea, Taiwan, and Venezuela.

The commercial fishery in nearshore waters can be described in terms of several main components which overlap slightly. The most important of these, both in weight and value, is the demersal fishes component, in which fish pots and hand lines are used to catch shallow reef species and deep-water snappers and groupers. This component of the fishery accounts for about 70% of the catch in Puerto Rico and 53% of its value. The second component of the fishery is for coastal pelagic fishes, using troll lines, beach seines, and gill nets; this component accounts for about 21% of the total catch and 16% of its value in Puerto Rico. Shellfish, the third component, accounts for only about 15% of the Puerto Rico catch but about 30% of its value. Spiny lobster landings are over 50% of the shellfish catch, yet 70% of its value; the other major shellfish species is the queen conch.

Although the economic importance of the recreational fishery has not been evaluated, it is of considerable importance to the tourism industry and the local residents. Its importance in Puerto Rico is reflected in a catch of 1,361 blue and white marlin and sailfish from May 1977 to April 1978, about half of which were caught by vessels from outside the area. Other species for which the area is known are yellowfin tuna, wahoo, bonefish, some of the larger reef species, and billfishes. Billfishes are already overexploited in the Atlantic, so the future of that recreational fishery is uncertain.

Eggs and Larvae of Important Species—Data on abundance and distribution of the early life stages of important species is rather scant; thus, it is difficult to make a general comparison of larvae from Hawaii and the Caribbean. Based on reproductive stages of adult fish in the Caribbean (Munro et al. 1973), it appears that reef fish eggs and larvae will be most abundant during February through April. However, the eggs and larvae of tuna and billfishes will be most abundant during the summer, with some species present at lower numbers in spring and fall (Matsumoto et al. 1984; Uchida 1981; Yoshida 1979; Shomura and Williams 1975; Miller et al. 1979; Idyll and deSylva 1963).

Spatial distribution of larvae is quite complicated depending on both the reproductive habits of the fish and water movement in and near the spawning area. Most of the important reef species have pelagic eggs and appear to be spawned at times and locations where the eggs will be quickly moved offshore to areas where predators may be less abundant. This pattern has been substantiated in Hawaii by Leis (1982) who found reef fish eggs were more abundant 3.0 km from shore than 0.2 km out, and Miller (1974) who reported larvae of some fish were more abundant 50 km off Oahu than 5 km out. Dekhnik et al. (1973) found the same larval pattern off Cuba and several studies have shown the same pattern with fish eggs at other Caribbean sites (Moore 1967; Sander and Steven 1973; Moore and Sander 1976). Larval distribution of pelagic species may be much different. Miller et al. (1979) reported tuna larvae were much more abundant nearshore and on the leeward rather than windward coast. It appears likely that high surface densities of larvae are produced by wind-driven upwelling of layers of water containing fairly dense larval concentrations.

Comparing absolute abundance of larvae between areas is particularly difficult because various investigators use different techniques, including sampling at different depths, and because the samples display considerable variability. The larval abundance of oceanic species in the Caribbean (Richards 1981), however, appears similar to that in the eastern tropical Pacific (Ahlstrom 1971, 1972). The Caribbean may have a more diverse assemblage with 15 families accounting for about 70% of the larvae (Richards 1984) in comparison to the Pacific, where 10 families constituted 90% of the larvae. It is likely that in both regions the larvae are most abundant nearsurface. In the mid-Pacific, Hirota (1977) found:

1) that the larvae of commercially important tuna occur more abundantly in the neuston layer than from 1-200 m,

2) the species in the 1-200 m layer are primarily midwater forms, and

3) very few larval fish occur between 200-1000 m.

Off Puerto Rico the vertical trend is similar with few fish below 200 m and the highest number between 0 and 25 m (Vargo et al. 1981).

Other Important Biological Components—Other biological components such as coral reefs, mangroves, and sea grass beds are all very important habitat types for numerous fishery resources, at least during some portion of the individual species' life cycle. Impacts on such fishery habitats may be of greater importance than direct impact on the species themselves (eggs, larvae, adults), particularly for near/onshore OTEC sites (J. Naughton, Southw. Region-West. Pacific Program Staff, Natl. Mar. Fish. Serv., NOAA, Honolulu, HI, pers. commun. 1984). In addition, the destruction of coral reefs can sometimes lead to an increase in the incidence of ciguatera poisoning, caused by the ingestion of fish contaminated with a paralytic neurotoxin of natural origin (see Research Priorities section). It is important that all efforts be made to minimize the impact of OTEC operations on such biological resources.

In a strict interpretation, protected species such as marine mammals may not be "fisheries" resources. However, they are important components of the biota at the potential OTEC sites and impacts on them will have to be evaluated on a thorough basis. As noted in Table 3, a number of species are listed as threatened or endangered in Hawaiian and Caribbean waters. The humpback whale,

Table 3.—Threatened (T) and endangered (E) marine species (Source: 50 CFR 17.11-12).

	Hawaii	Virgin Islands
Marine mammals		
Right whale *Balaena glacialis**	E	
Sei whale *Balaenoptera borealis*	E	
Blue whale *Balaenoptera musculus*	E	
Finback whale *Balaenoptera physalus*	E	
Humpback whale *Megaptera novaeangliae*	E	
Hawaiian monk seal *Monachus schauinslandi*	E	
Sperm whale *Physeter catodon*	E	
Caribbean monk seal *Monachus tropicalis*		E
West Indian manatee (Florida) *Trichechus manatus*		E
Sea Turtles		
Loggerhead sea turtle *Caretta caretta*	T	T
Green sea turtle *Chelonia mydas*	E	T
Leatherback sea turtle *Dermochelys coriacea*	E	E
Hawksbill sea turtle *Eretmochelys imbricata*	E	E (=carey)
Kemp's Ridley sea turtle (=Atlantic) *Lepidochelys kempii*	E	E
Olive Ridley sea turtle (Pacific) *Lepidochelys olivacea*	T	
Birds		
Newel's shearwater *Puffinus auricularis newelli*	T	
Hawaiian dark-rumped petrel *Petrodroma phaeopygia sandwichensis*	E	

*Not considered part of the normal cetacean fauna in Hawaiian waters.

Megaptera novaeangliae, one of the most abundant cetaceans in Hawaii, is an endangered species which migrates into Hawaiian waters in winter to breed. A second endangered species, the Hawaiian monk seal, *Monachus schauinslandi*, is present; however, the population resides in the Northwestern Hawiian Islands and away from potential OTEC sites. Of the five sea turtles that have been reported off Hawaii, the green sea turtle (*Chelonia mydas*) is the most abundant. A single green sea turtle has been observed repeatedly on the reef directly off the Kahe Point power station.

A number of marine species listed as threatened or endangered, including several turtles, are found in the waters off Puerto Rico and the Virgin Islands. Of particular importance are the leatherback and hawksbill turtles which nest in potential OTEC areas, and humpback whales which calve and mate in the region from January through April.

Factors That May Affect Fish

Organisms entrained by the intakes of an OTEC plant will either be impinged on screens placed to prevent larger objects from entering and clogging critical parts of the plant, or entrained and transported through the plant and then discharged. In passage through the plant, entrained organisms will be subject to a number of stresses such as temperature and pressure changes, and chemical additions. Upon discharge to the environment, entrained organisms will be redistributed in the water column along with additional organisms entrained into the discharge plume. The artificial upwelling of nutrients and other constituents contained in the deeper, colder waters and their subsequent redistribution may also effect some biological changes.

Attraction/Avoidance—The attraction or avoidance of fish towards objects, light and noise is a known phenomena that is expected to occur with OTEC operations, whether they be open-ocean plant-ships, stationary towers, moored platforms, or land-based plants. For the purpose of this study, Seki (1984) has summarized available information on this topic and related it to OTEC development; the following is a brief synopsis of his findings.

The attraction of fish to free-floating and anchored objects or structures has been studied throughout the world's tropical and subtropical waters. The objects with which fish have been observed to associate include drifting seaweed (Senta 1966), driftwood (Yabe and Mori 1950; Inoue et al. 1963; Hunter and Mitchell 1967; Inoue et al. 1968), manmade rafts (Kojima 1960; Gooding and Magnuson 1967), and artificial surface or midwater structures, including commercial fish aggregating devices (FAD's) (Hunter and Mitchell 1968; Klima and Wickham 1971; Wickham et al. 1973; Wickham and Russell 1974; Matsumoto et al. 1981). Tunas dominate the catch of the pole-and-line, trolling, handline, and purse seine boats fishing around FAD's, as evidenced by some catch data obtained from Kiribati, Western Samoa, Fiji, and Hawaii (Shomura and Matsumoto 1982). The experimental study by Matsumoto et al. (1981) provided the most detailed records of catches around FAD's in the Pacific. Matsumoto reported that skipjack tuna, *Katsuwonus pelamis*, represented nearly 90% of the catch by the pole-and-line boats. These fish ranged from 0.9 to 5.4 kg and sometimes over 9.1 kg. Unlike pole-and-line boats, trolling boats had a much more diversified catch. Tunas (mostly yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*) still dominated the catch, although mahimahi, *Coryphaena hippurus*, constituted the largest percentage of single species caught.

Another tuna fishery which utilizes FAD's (in conjunction with an artificial light source) in Hawaii is the ika-shibi or the night handline fishery for tuna. Although this rapidly growing fishery utilizes extremely simple gear (a single hook and a line) as compared with the longliners and large purse seiners, it is an extremely effective method as indicated by the mean catch rate of approximately two fish per hook per night (Yuen 1979).

In comparison to floating OTEC structures, the tower and man-made island designs of OTEC plants are expected to function as artificial reefs, duplicating those conditions that cause concentrations of fishes and invertebrates on natural reefs and rough bottom areas. The effect of tower designs would be similar to that of offshore oil platforms, which have resulted in an increase in offshore sport fishing in the immediate area.

Numerous studies have described the variety of fish which have been attracted to artificial reefs at various sites. In all studies, the many different species found generally represent similar basic broad behavioral classes, such as the Turner et al. (1969) reef or nonreef associates (the former further split into resident or semiresident). Four reefs were established at various sites in Hawaii between 1960 and 1973, using primarily car bodies, damaged concrete pipes, and old car tires filled with mortar. The southern boundary of a reef created on one of these sites (Waianae) on the western coast of the Island of Oahu is at lat. 21°25.1′N, long. 158°11.6′W (Kanayama and Onizuka 1973) only 3 miles from the present OTEC benchmark survey site at lat. 21°19.5′N, long. 158°12.5′W offshore of Kahe Point. Sampling along a fish transect established before the reef construction indicated the presence of 32 different species and a standing crop density of 103 pounds of fish per acre. The reef was constructed in two sections, one composed of car bodies and the other of damaged concrete pipes. Thirty species of fishes (standing crop estimated at 1,271 pounds/acre) were present at the car body section. This was a tenfold increase over the pre-reef count. The concrete pipe section showed a fivefold increase of 45 fish species and a standing crop estimated at 496 pounds/acre.

Although attraction of fish to man-made structures is well documented, questions still arise regarding the relationship between artificial structures and fish production. Mallory (1965) believed that a structure concentrated the fish which constantly migrated in and out, thus serving as an orientation point. This was true for a number of species (primarily the game fishes) associated with flotsam. Stroud (1965) felt that since the artificial habitat provides food and shelter, reproduction will be enhanced resulting in an increase in production and yield of fish. A third hypothesis discussed by Carlisle et al. (1964), Turner et al. (1969), and Dugas et al. (1979), combines both viewpoints; fish are concentrated by recruitment, and, as the colonization progresses on the structures, a reproducing resident fish community may evolve. Although this may hold true for many of the reef fishes, this hypothesis falls short of accounting for overall fish attraction as evidenced primarily for such species as the deeper water pelagic scombrids and billfishes.

The attraction of various marine organisms to light is a phenomenon that has been used in the harvesting of fish for many years. Mackerel scad, *Decapterus macarellus*, and bigeye scad, *Selar crumenophthalmus* (Yamaguchi 1953; Powell 1968), various species of tuna (Yuen 1979), and squid (Ogura and Nasumi 1976), are caught by the use of night lights. How much of an effect the lights from an OTEC facility will have on the tuna is not presently known. As indicated by Laevastu and Hayes (1981), every species has a particular optimum light intensity in which its activity is at a maximum. It is probable that the intensity of the artificial light would fall within the thresholds of some species.

Regarding avoidance traits of marine biota to structures and operations in the ocean, published information is virtually nonexistent. Yuen (1981) indicated that the endangered and threatened species would probably avoid the area due to human presence and to the noise emitted from the plant. Among the few studies that address avoidance was one on the negative phototactic behavior of fish. Dragesund (1958) found that herring would sometimes display a shock response. That is, when the light was turned on, the fish would make a sudden upward movement towards the light only to later disperse or school and descend. Studies on other aspects of avoidance, such as of the physical structures, are nonexistent in published literature. Future studies should be directed in this area.

Impingement—Impingement at coastal power plants has been an ecological problem (loss of a large number of organisms), an operational problem (reduction in cooling water flow), and a cost problem (removal and disposal of organisms). Impingement occurs when organisms too large to pass through the intake screen, are pulled against it, and are unable to escape due to the current velocity. Schooling fishes are especially susceptible, and impingement mortalities may involve millions of individuals. In one incident, 2 million menhaden at the Millstone Plant in Connecticut were impinged and caused a shutdown of the plant by reducing the cooling water flow. These mortalities are believed by some ecologists to be reaching proportions which may cause population damage (Van Winkle 1977). As a result, data on impingement of fish have been collected from many operating plants (Adams 1969; Marcy 1971; Jensen 1974; Uziel 1980).

Variation in impingement on intake screens is related, among other things, to season, swimming speeds, intake location, and operating schedules of the power plant. Screen catches at most coastal power plants studied in temperate waters fluctuate markedly with season, due to migrations into and out of intake areas and to changes in water temperature that affect the fishes' ability to swim successfully against intake currents. In tropical areas, where OTEC plants will be located, impingement may be less variable because there is generally less migrational movement of populations and the water temperature is essentially the same the entire year.

The swimming speed of an organism determines whether or not it will escape impingement or entrainment once in the vicinity of an intake. Eggs and larvae of marine fish drift passively in the ocean within the zooplankton community. Early larval stages utilize swimming only to capture prey, escape predation, or migrate vertically. In general, sustained swimming speeds of fish larvae fall into a range of 2-4 body lengths/second for larvae in advanced development or for juveniles (Blaxter 1969; Bainbridge 1960). Table 4 lists representative species, including a few freshwater species, for individuals up to 6 cm in length. For most fishes, relative speeds decrease as size increases above that shown in Table 4, and absolute speed increases as size increases.

Table 4.—Sustained swimming speeds of some larval and juvenile fish species (adapted from Marcy et al. 1980).

Species	Length (mm)	Speed (mm/s)	Temp (°C)	Time maintained	Body lengths per second	Author
European plaice	7.5	12	6.5-7.5	A few s	—	Ryland (1963)
	9.5	27	6.5-7.5	A few s	—	
Whitefish	10-12	16	4	?	1.6	Braum (1964)
		29	16	?	2.4	
Common roach	35-45	138	?	1 min	3.1-3.9	Aslanova quoted by Radakov (1964)
Common bream	45-55	126	?	1 min	2.3-2.8	
Carp	50-60	129	?	1 min	2.1-2.6	
Horse mackerel	30-40	136	?	1 min	3.4-4.5	
Mullet	35-45	128	?	1 min	2.8-3.6	
Mullet	45-55	156	?	1 min	2.8-3.5	
White bream	18-26	330	?	?	12.7-18.3	Radakov (1964)
Atlantic herring	6.5-8	5.8	?(14)	45 min	0.7-0.9	Bishai (1960)
Atlantic herring	12-14	10	9-10	60 min	0.7-0.8	Blaxter (1966)
Sole	4	6-9	15	Long periods intermittent swimming	1.5-2.2	Rosenthal (1966)
Bleak 0.26 g	(wet wt)	29.8	20	—	—	Ivlev (1960)
Smallmouth bass	22	146-312	20-35	3 min	6.6-14.2	Larimore and Duever (1968)
Yellow perch	6.5	5.5	13	60 min	0.8	Houde (1969)
	7.5	14.0	13	60 min	1.9	
	8.5	24.0	13	60 min	2.8	
	9.5	27.5	13	60 min	2.9	
	10.5	32.0	13	60 min	3.0	
	13.5	46.0	13	60 min	3.4	
Walleye	7.5	5.0	13	60 min	0.7	Houde (1969)
	8.5	13.0	13	60 min	1.5	
	9.5	29.0	13	60 min	3.0	
	10.5	32.0	13	60 min	3.0	
	11.5	37.5	13	60 min	3.3	
	13.5	42.0	13	60 min	3.1	
	14.5	46.0	13	60 min	3.2	
Lake whitefish	15.2	35	7.5	1 min	2.4	Hoagman (1974)
	15.8	58	11.5	1 min	3.7	
	19.7	71	11.5	1 min	3.6	
	21.3	76	14.5	1 min	3.5	
	28.8	115	14.5	1 min	4.0	

Among the fastest burst swimmers are yellowfin tuna, which as adults can swim 27 body lengths/s for 5 seconds (Walters and Fierstine 1964). Although larvae do not have strong sustained swimming ability, they possess impressive darting or burst speeds relative to their size. Blaxter (1969) suggests bursts of 10 body lengths/s which, for most larvae (up to 25 mm), would limit their speed to less than the 0.25-0.30 m/s suggested as typical of OTEC plant warm-water intake velocity (see Seawater Systems section). Scombrid larvae have not been measured for burst swimming performance, but Pacific mackerel up to 3.6 cm in length swam up to 26 cm/s, counting time spent in rest and feeding (Hunter 1980).

Swimming ability is a function of morphological shape, stage of development, length, ambient temperature and light, and the duration required for the performance (Tsukamoto et al. 1975; Hartwell and Otto 1978; Rulifson 1977; Pavlov et al. 1968; Larimore and Duever 1968; Hunter and Kimbrell 1980). Knowledge of these factors and the types of species likely to be near the OTEC plant site is necessary to predict the potential of larvae and juveniles to escape intake currents.

Morphologically, the fastest species have a high aspect ratio of the caudal fin (ratio of the square of the caudual fin depth to the surface area) (Lighthill 1970). Species with high aspect ratios are those with the carangiform (e.g., Carangidae, Clupeidae, Pomatomidae) and thunniform (e.g., Scombridae, Istophoridae, Xiphiidae, Stromateidae) swimming motion. Anguilliform swimmers (e.g., Anguillidae, Pleuronectiformes), subcarangiform swimmers (e.g., Gadiformes, Salmonidae), or ostraciiform swimmers (e.g., Ostraciidae, Tetraodontidae, Lophiiformes) have a low caudual fin aspect ratio and are relatively slow.

The effects of temperature on swimming speeds are probably unimportant in predicting susceptibility of small fish to entrainment in an OTEC plant. While Hettler (1979) found that a 10°C increase in temperature caused the swimming speed for two carangiform juveniles to increase by a factor of 1.6, the relatively consistent temperature in the tropics is unlikely to cause large seasonal changes in susceptibility to entrainment.

The design of the water intake structure will greatly affect current velocity. It has been shown that fish are better able to orient to a horizontal flow than a vertical flow. Intake structures placed or capped so that intake flows are in the horizontal plane enable fish to orient to the flow and more effectively avoid the intake (Langford 1983).

Because of the large volume of water required by OTEC plants and the relatively high flow rate at the screens, impingement of organisms on the warm-water intake screens will assuredly be a visible effect and may, in some cases, be ecologically important. Impingement rates will depend on intake location and velocity, time of day, behavior characteristics of the populations of organisms associated with the plant site and, to some extent, season of the year, although this will be a relatively minor factor in tropical waters. Another important factor is that the plant may serve as a fish-attracting device and concentrate large numbers of organisms where they are in danger of being impinged or entrained (Seki 1984).

Impinged organisms generally fall into the micronekton size category (2-20 cm) and include fishes, macroplanktonic crustaceans, cephalopods, and gelatinous organisms such as coelenterates, salps, and ctenophores. Micronekton are an important intermediate step in the food chain between the zooplankton and commercially important fishes. The significance of large-scale mortalities due to impingement at coastal power plants in temperate waters has not been quantified from field data and there is presently no conclusive evidence of actual population declines in any species due to impingement losses.

Attempts have been made to model the effects on populations (see section on Potential Range of Ecological Effects) but there is, in general, a lack of needed data on natural mortality rates. In general, the data base for tropical-subtropical waters is even more deficient than for temperate waters. Very few quantitative studies have been made in tropical-subtropical waters to systematically collect samples of micronekton. Therefore, it is very difficult to estimate the impingement rate. Sullivan and Sands (1980), using data from water off Oahu, Hawaii, estimated a daily impingement of 420 kg for the warm-water screen of a 400-MWe OTEC plant, and concluded that this loss is probably insignificant when the replacement ability of the micronekton population in the surrounding region is considered.

Primary Entrainment—Any organism small enough to pass through the intake screens (approximately 1.3 cm; Sands 1980) will be entrained in the seawater flowing through the heat exchangers (primary entrainment). During this period, organisms are subjected to thermal and mechanical stresses as a result of changes in pressure and temperature, shear and acceleration forces, abrasion, and collision with structures. In addition, organisms will be subjected to biocides used to clean the surfaces of the heat exchangers, anti-corrosion agents, and corrosion products. Effects on organisms will be due to a combination of these factors.

The effects of primary entrainment at conventional power plants have been extensively studied and a number of reviews have been reported (e.g., Schubel and Marcy 1978). There is general agreement that while a great many species of organisms cannot survive passage through the cooling water system, there is a wide range of tolerance among species, and plant design and operating characteristics are critical factors. Mechanical damage is probably the major single factor contributing to primary entrainment mortality. The importance of thermal and chemical stress will vary depending on thermal exposure, biocide treatments, and corrosion rates.

Entrainment effects associated with OTEC will no doubt be one of the most important factors to consider with respect to fisheries. Because of the low thermal efficiency of OTEC plants the amount of water needed is extremely large; generally between 6 and 10 $m^3 \cdot s^{-1} \cdot MWe^{-1}$ for the total combined warm and cold water flow (see Seawater Systems section), as compared to an average of 0.05 $m^3 \cdot s^{-1} \cdot MWe^{-1}$ for condensing water for a nuclear plant. Because of this large water requirement, the number of organisms subject to entrainment will be large.

Temperature—Organisms entrained in conventional power plants are subjected to rapid increases in temperature as they pass through power plant condensers. The near instantaneous temperature changes (ΔT) may range from less than 6°C to more than 19°C (Schubel and Marcy 1978), and the exposure time to these elevated temperatures may range from several minutes to an hour (including time in the discharge canal) depending on the plant design. Laboratory research on the larvae of four species of temperate subtropical marine fish (Atlantic menhaden, *Brevoortia tyrannus*; spot, *Leiostomus xanthurus*; pinfish, *Lagodon rhomboides*; and flounder, *Paralichthys* sp.) has shown that their survival following entrainment in a once-through cooling water system will depend on the increase in condenser water temperature over ambient water temperature and the length of exposure (Hoss et al. 1971, 1974).

Studies designed to evaluate a hypothetical offshore conventional power plant with a ΔT of 10-12°C and an ambient temperature of

15-16°C indicate that spot, *Leiostomus xanthurus*, eggs may be more affected by heat shock during their first day of life than at later stages as embryos (Hettler and Coston-Clements 1978). Eggs of black sea bass, *Centropristis striatus*, did not show this same effect, so it appears that stage of development at time of shock may be important, but must be determined on an individual species basis. Spot eggs that were slowly returned to ambient temperatures had a much better survival than those subjected to a rapid return. The larvae of spot (1-21 days old) showed no apparent relationship between age and survival following thermal shock (Hettler and Coston-Clements 1978).

Unlike conventional power plants where organisms experience only an increase in temperature as they pass through the condensers, organisms entrained in OTEC plants will experience both increases and decreases in temperature. Organisms entrained in the warm water will pass through the evaporator, where the temperature will be decreased by 2-3°C, while organisms entrained in the cold water will pass through the condenser, where temperature will be increased 2-3°C (U.S. Dept. of Energy 1978). Additionally, organisms will be subject to larger temperature changes upon mixing of the two effluents (if practiced) and/or discharge to the environment. For instance, a mixed discharge would effect a temperature drop of about 10°C for the warm-water organisms and a 10°C increase for any cold-water organisms. Entrained organisms will also experience a redistribution in the water column when discharged with effluent waters. This redistribution could also expose organisms to a different temperature regime.

No literature was found on cold shock in fish for the temperature range and ΔT expected for the OTEC discharge. Cold shock literature is limited to describing effects of rapidly reduced temperatures during the cooler months to new temperatures at or near the low lethal temperatures, which produce death by the formation of ice in the tissues or induce primary (respiratory) or secondary (nerve blockage) chill comas. All reported fish kills or experimental cold shocks involved species in temperate climates. Chittenden (1972) found that young *Alosa sapidissima* exposed to abrupt temperature decreases from 24°C to 12°C were not affected, but below 12°C even gradual decreases caused sublethal behavioral problems. Terpin et al. (1977) showed that *Anchoa mitchilli* died at 10°C when acclimated to 22°C and subjected to a 12°C decrease in 29 hours. However, no mortality occurred at decreases of 4°C and 7°C. Becker et al. (1977), although not working with marine species, showed that differences in response to abrupt temperature changes were found between species, inferring that a general prediction of the effect of cold shock cannot be made to a number of species. Further, knowledge of thermal requirements of the adults of a species may not be sufficient to predict those of egg and larval forms. In Brett's (1956) review, he states that ". . . the thermal requirements in the very early stages are more exacting than in the adult." For eggs and larvae of stenothermal species, reduced temperatures, although not actually "cold," will retard development and may cause abnormalities. Harada et al. (1978) found that no yellowfin tuna larvae developed normally in temperatures below 20°C.

Pressure—Rapid change in hydrostatic pressure is one of the stresses to which organisms are subjected during entrainment. These pressure changes may be either negative (vacuums within the pump) or positive, and the magnitude of the change is dependent on design of the plant.

It has been suggested that rapid changes in pressure that occur in power plant cooling water pumps may be potentially damaging to entrained fish (Marcy et al. 1980). Although much research has been conducted on the effect of pressure change on fish, very little of it has any direct relevance to the relatively small pressure changes (1-5 atmospheres; 1 atmosphere change equivalent to a 10-m depth change) to which fish are subjected in power plant cooling systems.

Much less entrainment of organisms is expected in the cold water intake of an OTEC plant, but any entrained organisms will be exposed to a pressure change of 70-100 atmospheres depending on depth of the intake pipe. Entrained fish larvae possessing a swim bladder would be very vulnerable to rapid changes in pressure of this magnitude (Hoss and Blaxter 1979; Blaxter and Hoss 1979).

Chemical Additions—Due to the low thermodynamic efficiencies available through the OTEC system (Myers and Ditmars 1985), the heat transfer rate at the heat exchanger surfaces will be critical. The inhibition of biofouling due to microorganisms must thus be an integral aspect of OTEC operations. As in coastal power plants, current thought here supports the need for intermittent chlorination to keep biofouling to a sufficiently low level. As noted by Hoss and Peters (1983), there is concern over the use of chlorine because of its toxicity. It has been shown that added chlorine can seriously affect the growth and survival of entrained organisms (Schubel and Marcy 1978), although there are species-to-species variations and certain synergistic effects with temperature and trace metals (Hoss et al. 1975, 1977).

The biocide concern is amplified in an OTEC operation because of the large volumes of water involved, i.e., the achievement of a certain concentration for biocidal effectiveness will require the application of large quantities of biocide. Although the required dose of chlorine will be somewhat site-specific, recent studies indicate that concentrations of total residual chlorine of about 0.07 mg/L may achieve the desired results (Larsen-Basse and Daniel 1983). This is well below the new source performance standards (NSPS) requirement for chlorine discharges from steam electric generating stations, the standards which would most likely apply to OTEC discharges (Myers and Ditmars 1985). For plants with a steam electric generation capacity of 25-MWe or more, the NSPS specify the total residual chlorine (TRC) in the cooling water discharge from any single generating unit shall not exceed 0.20 mg/L, and that the duration of chlorine discharge shall not exceed 2 hours/day.

Although chlorine bioassay studies by Venkataramiah et al. (1981b) suggest that levels less than or equal to 0.5 mg/L may be generally safe, there are still concerns regarding cumulative effects of continuous discharges that must be further addressed (Venkataramiah et al. 1981a; U.S. Department of Energy 1981). There is also a potential for synergistic reactions of chlorine with trace metals and ammonia leaks. Recent studies (Venkataramiah et al. 1981a,b) on marine fishes and zooplankton have shown that the toxicity of ammonia and chlorine varies with habitat of the species and with duration of exposure. Within the same species (gray mullet, *Mugil cephalus*), smaller fish were more sensitive than larger fish. This work confirms past research on other species and provides further evidence that exposure to chlorine in marine waters, while not well understood, may present a serious problem and should receive additional study.

Because of the large surface areas required for OTEC heat exchangers [about 9.3 m^2/kWe for closed cycle (NOAA 1981a)], heat exchangers are considered one of the principal sources of trace metal release. Myers and Ditmars (1985) have used the results of DOE-supported corrosion tests (Tipton 1980) to make worst-case estimates of trace metal concentrations in OTEC discharges (Table 5). In general, the concentrations of trace metals in an OTEC

Table 5.—Estimates of OTEC effluent trace metals concentrations due to heat exchanger corrosion and erosion.

Material[a]	Cleaning environment[b]	Material loss/unit area 3-mo exposure[c] (mg/cm^2)	Trace constituent concentrations in OTEC discharge effluent[d] (ng/g)
Alclad 3003	Brush + chlorine	34.3	Al, 66; Zn, 1
5052 Al	Brush + chlorine	10.1	Al, 19; Mg, 0.49; Cr, 0.05
CA 706 Cu-Ni	Brush	87.5	Cu, 151; Ni, 17; Fe, 2.4
Al-6X Steel	Brush	0.02	Fe, 0.02; Ni, 0.01; Cr, 0.01; Mo, 0.002
Ti	Brush	<0.01	Ti, <0.02

[a] Material composition: Alclad 3003 is 99% Al, 1% Zn; 5052 Al is 97.5% Al, 2.5% Mg, 0.25% Cr; CA 706 Cu-Ni is 88.6% Cu, 10.0% Ni, 1.4% Fe; Al-6X Steel is 50% Fe, 24% Ni, 20% Cr, 6% Mo; and titanium is commercially pure.

[b] Cleaning environment is either M.A.N.® (American M.A.N. Corp., N.Y.), brushing with 3 round-trips/day or brushing plus continuous chlorination at 0.1 mg/L concentrations.

[c] From Tipton (1980); largest alloy losses from 3-mo exposure reported here.

[d] Calculated assuming alloy loss (from Tipton 1980), heat exchanger surface areas of 9.3 m^2/kWe (NOAA 1981a), and OTEC seawater flows of 6 m^{3}s^{-1}MWe^{-1}.

discharge are estimated to be on the order of 100 ng/g (100 μg/L) or smaller. With the possible exception of copper, these estimates suggest that the release of trace metals from heat exchanger surfaces would not pose significant concern. Worst-case estimates of the release of copper from a Cu-Ni alloy (i.e., CA 706) indicate concentrations above 100 ng/g, in the acute toxicity range of copper in seawater based on a number of observations of copper toxicity (Klapow and Lewis 1979).

With the exception of catastrophic accidents, any leaks of working fluids will be diluted by the large volumetric flow of seawater through the plant, to the point that problems should not arise. For instance, with the Ocean Thermal Corporation OTEC design for Kahe Point, it is predicted that normal leaking of ammonia could result in an increase of 2.4 μg/L above the ambient level of 10.7 μg/L in the mixed discharge (Ocean Thermal Corporation 1983). Upon reaction with the seawater, only about 5% of this increase would remain as un-ionized ammonia, the principal toxic form. The concentration of un-ionized ammonia in the discharge would then be about 0.66 μg/L, well below a reported minimum-risk level of 10 μg/L (U.S. Environmental Protection Agency 1973) and only 0.12 μg/L greater than the ambient concentration of un-ionized ammonia.

Secondary Entrainment—Secondary entrainment refers to the capture of organisms in discharge waters (effluent plume) as a result of turbulent mixing or behavioral responses. The rate at which organisms are entrained in this manner will depend on the discharge flow rate, the near-field dilution, and the average population density along the near-field trajectory of the plume (Paddock and Ditmars 1983).

Most of the same stresses encountered in primary entrainment will also be encountered in secondary entrainment, the difference being that the magnitude of the stress will, in general, be much less. Determining the effects on fisheries organisms of secondary entrainment will be even more difficult than for primary entrainment, and results from previous power plant studies are limited in their usefulness.

Ehrlich (1977) reported that the hatching success of California grunion (*Leuresthes tenuis*) was significantly reduced by a nonthermal but unknown component of the effluent from a California power plant. Large variation in hatching success suggested that the unknown hatching inhibitor in the water fluctuated during plant operation. It is possible that trace metals in the effluent caused the variation, since previous work by Rosenthal and Alderdice (1976) showed reduced hatching in herring eggs exposed to trace metals. The effects of small changes in water temperature have been shown by Peters and Angelovic (1973) to be an important factor in controlling fish feeding and growth. Small changes in temperature (either increases or decreases) in the discharge plume may, therefore, have an effect on larval fish growth, but this will be very dependent on the depth at which the discharge occurs and the total area that is impacted.

Ocean Water Mixing—An OTEC plant's displacement of large quantities of deep ocean water can cause an upwelling effect that may disturb the natural temperature structure, salinity gradient and levels of dissolved oxygen, nutrients, and trace metals in the surface waters. Artificial upwelling is not a characteristic of conventional power plants; therefore, there is little direct analogy to the OTEC situation. However, some studies that have been made on nutrient distribution and changes in trace metal levels may be of some use in predicting upwelling effects.

In general, it is thought that the pumping of large amounts of deep nutrient-rich ocean water to the surface layer may have positive effects if the same type of biostimulation occurs near OTEC plants as occurs near areas of natural upwelling. However, whether upwelling will be harmful or beneficial to local ecosystems will depend on many factors, as discussed in the section Impacts on Fishery Food Chains.

The concentration of trace metals in surface water may increase due to upwelling of metal-rich deep water or the formation of corrosion products. The impact of these increases will depend in large part on the amount and chemical form of the metals involved. The free ion activity, not the total metal concentration, determines biological availability and effect. Increases in the bioavailability of micronutrients, e.g., iron, manganese, and copper, could increase production of the algae community. Similarly, toxicity could result from high availability of metals, such as copper, zinc, or cadmium, which could be detrimental to biological production. If the trace metal complement of the effluent water is harmful, the potential biostimulatory effect of upwelled nutrients may either not occur or be unnoticeable. The trace metal complement will change with time through a variety of processes, and a bloom may be merely delayed. With current information it is not possible to predict what effect the altered trace metal regime will have on the utilization of upwelled macronutrients, nor is it clear whether the effects will differ with location.

The Potential Range of Ecological Effects Resulting From OTEC Operations

Marine ecosystem impacts which may result from OTEC operations can be described only in very general terms. This section attempts to estimate the upper and lower bounds of these effects for a 40-MWe shorebased plant with the effluent plume coming to equilibrium near the bottom of the mixed layer (see Effluent Discharge section). Impacts which we consider include impingement, primary and secondary entrainment, and nutrient enrichment. This or any estimate of impacts is limited by the environmental data available and by an incomplete understanding of the amounts and types of ecological compensation which may occur. Also, evaluating the importance of projected effects will be particularly difficult and dependent upon resource and system boundaries.

Impingement—Impingement rates will depend on volume and speed of the intake waters and the abundance of animals larger than the mesh size of the intake screen and their ability to avoid the intake. An animal's ability to avoid the intake depends on (1) rheotactic behavior, (2) visual perception in low light environments, and (3) swimming speed. Swimming speed depends on (a) species limitations (form or hydrodynamics), (b) temperature, and (c) physical condition. Physical condition depends on (i) nutritional state, and (ii) presence of disease or injury. While neither abundance or avoidance capability is well documented, reasonable estimates are possible. Fish, in general, can swim about 3-6 body lengths per second and will avoid intakes which are visible and in a horizontal flow field (Hocutt and Edinger 1980). With estimated intake velocities of 0.25 to 0.30 m/s (see Seawater Systems section), it is unlikely that fish over 10 cm in length will be impinged, and many smaller ones could probably avoid the screens. The minimum length of fish impinged will be several times the screen mesh size. Thus, most impinged animals will be in a size range probably narrower than from 3 to 10 cm.

While there are no measurements of the absolute abundance of animals susceptible to impingement by an OTEC plant, trawl surveys conducted near Hawaii (Maynard et al. 1975) and Puerto Rico (Vargo et al. 1981) may be used to provide estimates of impingement rate. While catch efficiencies of the trawls are not known, we assume the fishes' susceptibility to capture by net is about the same as by impingement. Although the nets were pulled several times faster than plant intake velocities, most animals caught were of the same small size (<10 cm) which is most susceptible to entrainment or impingement. By adjusting the reported trawl catches for items identified as undersized or soft-bodied (entrainable rather than impingeable) and oversized (those which can probably avoid an intake), we can estimate expected impingement.

In both areas surveyed, fishes were the most abundant group, with crustaceans and cephalapods also present. In Hawaii surface-waters, a combined catch of all three groups was 0.2 mg/m^3 during the day and 5.4 mg/m^3 at night. Micronekton sampling near Puerto Rico revealed an average biomass of 2.7 mg/m^3. Adjusting the Caribbean catch for the 60% "residue" of entrainable size organisms, which those samples contained, results in estimates of 1.1 and 2.5 mg/m^3 for day and night, respectively, or an average 1.8 mg/m^3 of animals large enough to get caught on surface intake screens. In these samples, there appeared to be few animals which were large enough to escape intake velocities. In Hawaii the net was pulled faster than in Puerto Rico (1.7 vs 1.0 m/s) and larger animals were collected. Adjusting the nocturnal catch in Hawaii for those fish weighing more than 10 g (those most likely to be able to avoid impingement) results in estimates of the biomass of animals which will be impinged at night (4.6 mg/m^3). The average impingeable biomass over a 24-hour period is 2.4 mg/m^3. Similar calculations with data from deeper water result in an estimate of impingeable biomass at the cold water intake of 3.4 mg/m^3 in the Caribbean and 4.2 mg/m^3 in Hawaii.

Multiplying the average concentrations of impingeable biomass from the two studies (2.1 mg/m^3 at the surface and 3.8 mg/m^3 in deep water) times estimated flow rates results in an estimate of impingement rates. A 40-MWe plant with surface and deep intake rates of 120-200 m^3/s (i.e., 3-5 $m^3 \cdot s^{-1} \cdot MWe^{-1}$ for each intake; see Seawater Systems section) would probably impinge 20-35 kg live weight daily from the surface water and another 40-65 kg at the cold water intake, roughly in accord (being an order of magnitude less) with the impingement estimated by Sullivan and Sands (1980) for a 400-MWe OTEC plant in similar waters (see Impingement section). These estimates of impingeable biomass are based on the assumption that larger organisms can detect and avoid the intake screens. We are unaware of any measures of the concentration of larger organisms which could be used to estimate impingement rates on a screen which they could not detect; thus, our estimates can serve only as a lower bound. Higher rates are possible, but we have no means of estimating them.

Primary Entrainment of Plankton—Plankton entrainment rates are a function of plankton density and the rate of water intake. While the intake rate can be predicted and information on average density of various planktonic groups is available, their vertical stratification is, in many cases, not clearly documented. Those motile organisms which aggregate at particular depths may be entrained at rates vastly different than predicted from their average density in the mixed layer.

Phytoplankton biomass is approximately the same in Hawaii and the Caribbean. In the mixed layer at the Hawaiian Kahe Point OTEC site the median value was 0.10 mg chlorophyll-*a*/m^3 (Uchida 1983). The average of eight published values reported from the Caribbean surface waters (Hoss et al. 1983) is 0.13 mg/m^3. Judging from chlorophyll-*a* concentration at discrete depths, there is no consistent pattern in the vertical distribution of phytoplankton in the upper 50 m near Hawaii and Puerto Rico (Sands 1980). Thus, average concentrations can be used to estimate phytoplankton entrainment. However, it should be recognized that while mean abundances in Hawaii and the Caribbean are similar, individual measurements showed considerable variation, so the rate of entrainment of phytoplankton may also vary widely over time. To be conservative in estimating the range, extreme lower and upper bounds are assumed to be 0.05 mg/m^3 and 0.25 mg/m^3.

Daily phytoplankton entrainment by a 40-MWe plant, again with surface and deep-water intake rates each in the range of 120-200 m^3/s, will probably be between 0.5 kg chlorophyll-*a* (0.05 mg chlorophyll-*a* m^3 and 120 m^3/s) and 4.3 kg (0.25 mg chloropyll-*a* m^3 and 200 m^3/s). Assuming a factor of 100 for relating chlorophyll-*a* to organic carbon (Holm-Hansen 1969), we estimate that the organic carbon of phytoplankton entrained will be in the range 50 to 430 kg C/d. If the chlorophyll-*a* concentration is 0.1 mg/m^3, a figure frequently used to describe subtropical oceanic water, then phytoplankton entrainment will be in the range 100 to 170 kg C/d.

The zooplankton biomass which is subject to entrainment by an OTEC plant consists of two major fractions: macroplankton caught in conventional nets (200 μm or larger mesh) and microplankton small enough to pass through such nets. The larger animals in surface waters have been studied enough that their density is fairly well known. In Hawaiian water the mean dry weight biomass in the upper 200 m was 4.9 mg/m^3 and 3.3 mg/m^3 in two different sets of cruises (Noda et al. 1981b, from Uchida 1983). The average of four published studies from the Caribbean is 2.6 mg/m^3 (standard error = 0.24). Converting these dry weights to nearsurface zooplankton carbon (Wiebe et al. 1975) yields estimates of 1.3 mg C/m^3 in Hawaii and 0.8 mg C/m^3 in the Caribbean. Macrozooplankton abundance at cold-water intake depths has not been studied as thoroughly as at the surface. The concentration clearly decreases with depth and will probably be less than 0.24 mg C/m^3 (Table 6). The 0.24 mg C/m^3 average estimated from four studies (Table 6) is probably inflated because many of the samples were taken during the day when plankton abundance is greater than the 24-hour average and because we chose the highest of the conversion factors reported for estimating dry weight.

The smaller zooplankton, i.e., microzooplankton, have received little study so estimates of their density are not very precise. While microzooplankton density appears to vary with depth, we averaged measurements from the top 100 m of the photic zone as an indicator of entrainable biomass. A study in Hawaii (Gundersen et al. 1976) showed an average biomass of 0.7 mg C/m^3. Holm-Hansen (1969) reported values off southern California of 0.9 mg C/m^3. Using 0.08 as a factor to convert displacement volume to carbon (Holm-Hansen 1969) and the volumes given by Beers and Stewart (1969, 1971), we calculate the microzooplankton biomass averaged 2.3 mg C/m^3 in the eastern tropical Pacific and 1.2 mg C/m^3 in the California current. From these estimates it appears that microzooplankton abundance is approximately the same as the average macrozooplankton density in Hawaii and the Caribbean (about 1 mg C/m^3). This similarity in biomass of these vastly different sized animals has also been noted by Sheldon et al. (1977). With little information indicating the factors responsible for differences in density of microplankton, a more precise estimate of abundance in surface water is not possible.

With micro- and macrozooplankton densities in the mixed layer each averaging about 1 mg C/m^3, the warm water intake of a 40-MWe plant will entrain between 10 and 17 kg C/d in each of the zooplankton size categories. For the lack of evidence that microplankton are abundant at such depths, we assumed that entrainment at the cold water pipe will be limited to macroplankton. If deeper water macroplankton are present at a density of 0.2 mg C/m^3 (Table 6), then entrainment will probably range from 2 to 4 kg C/d.

Secondary Entrainment—Turbulent mixing will result in a rapid dilution of the effluent water through the entrainment of ambient water (see Effluent Discharge section). As a result, there is a potential for impact on the plankton present in the ambient water as they become entrained into the discharge plume. While it is difficult to predict the scale of impact from this secondary entrainment, the potential effect is considerable. This impact will depend on the abundance of organisms in the dilution water, their sensitivity to the altered water quality, and the amount of water involved.

Secondary entrainment will occur over a narrow depth range. Because of the desire to avoid recirculation of effluent back into the warm-water intake, the discharge location may be below 30 m. Based on the density of the effluent, relative to the density and density gradient of ambient waters near the discharge, the plume will come to equilibrium near the bottom of the mixed layer. Thus, it appears that the dilution water and therefore secondary entrainment of organisms will generally be from depths between 30 and 80 m. However, some recent modeling investigations (Wang 1984) indicate that there may also be an induced upwelling from beneath the plume which would entrain some water from below the mixed layer (see Regional Influence section).

Table 6.—Estimated macrozooplankton carbon density at cold water intake depth.

Area	Source	Depth of samples (m)	Data provided	Calculated (mg C/m^3)
Hawaii	Uchida 1983	200-1000	0.80 mg dry wt/m^3	0.26
Pacific (19°C) and Sargasso Sea	Vinogradov 1968	700	0.004 ml/m^3	0.17
Puerto Rico	Vargo et al. 1981	600-1000	0.0035 ml/m^3	0.15
Sargasso Sea	Deevey and Brooks 1971	500-1000	0.0108 ml/m^3	0.45
		1000-1500	0.0046 ml/m^3	0.19

Calculations used the following conversions: wet weight = 72% of displacement volume; dry weight = 13% of displacement volume; carbon weight = 32% of dry weight (Wiebe et al. 1975)

Several characteristics of the effluent (e.g., reduced water temperatures, the presence of a biocide, and a supersaturation of nitrogen gas) may adversely affect secondarily entrained organisms. Assuming a mixed discharge, we estimate that the temperature of the effluent at the point of discharge could be as low as 15°C. While many of the organisms which could be secondarily entrained engage in vertical migrations which expose them to a wide range of temperatures, others, including some of the ichthyoplankton, are not accustomed to such low temperatures. Even thermally tolerant, temperate organisms may be immobilized or killed by sudden exposure to cold temperature (Hoss et al. 1974; Bradley 1978; Stauffer 1980). The probability of mortality is greatest when the animals are living near their lower lethal limit. While most of the important tropical organisms have not been studied for thermal effects, it seems likely that many of those found in surface waters are stenothermal (e.g., tuna larvae) and may be impacted by temperature changes during secondary entrainment.

While biocides will probably be introduced only intermittently and at low concentrations, it is reasonable to assume that if the biocide is concentrated enough to kill fouling organisms it may also affect the more sensitive animals which are secondarily entrained. Prediction of biocide impacts from current information is difficult because most research has involved temperate organisms. Conducting additional research on biocide effects will be difficult because likely effluent concentrations are near the limit of detectability. Whatever biocide effects occur will be greatest in the zone of initial dilution where their concentration is greatest and thermal impacts are largest. Furthermore, previous research has shown that thermal and chlorine effects are synergistic (Hoss et al. 1977). There is also a possibility that temperature or chlorine effects may interact with effects from gas supersaturation. When saturated cold water is brought to the surface and warmed, it will be supersaturated with nitrogen, a condition which has caused fish mortality at other types of power plants.

With all the uncertainty surrounding the effects of water quality on secondarily entrained organisms, any prediction of effects is largely subjective. Until additional information is collected, it is assumed that cold shock effects will be insignificant for short-term temperature drops of less than 2°C, even in combinations with biocide concentrations and nitrogen supersaturation 20% that at the point of discharge. If surface and deep water intake rates are equal, the total discharge rate will be twice the surface intake rate. Assuming the temperature of the mixed layer to be constant, the amount of dilution water required to reduce the temperature difference to 2°C would be 8 times the surface intake rate (a 5:1 dilution being needed to decrease the difference between effluent temperature and ambient temperature to 2°C). With the further assumption that the concentration of biota in the depth interval of 30 to 80 m is the same as used in estimating primary entrainment mortality, an upper limit on secondary entrainment mortality may then be about 8 times that lost to surface primary entrainment. If cold shock rather than exposure to biocides, trace metals, or pressure changes is the major factor involved in the harmful effect of secondary entrainment, then many species may suffer only slightly, the most vulnerable being non-migratory animals. This, unfortunately, includes many fish larvae.

Impacts on Fishery Food Chains—Increased fish production can occur through either more primary production or shorter food chains, either of which could result from upwelling of nutrient-rich deep water. Primary production changes will in large part be due to the reaction of algae to nutrient and trace metal characteristics of the effluent plume. If these characteristics stimulate algal growth, fast growing diatoms will in all likelihood account for most of the production (Sunda and Huntsman 1983). If these diatoms are large or chain forming species they can probably be utilized directly by macrozooplankton. This could result in a shorter food chain than would occur if small algae were eaten by microzooplankton which were then eaten by macrozooplankton. Removal of one trophic step could increase fish production 5 to 10 times in the receiving waters.

In general, complex food webs, which occur in potential OTEC areas, are resilient so that most changes have little impact on ecosystem function. Minor changes in the food web, however, may drastically alter our acceptance of the fish produced. For example, blooms of the dinoflagellates which cause red tide or ciguatera can make the fish inedible. Unfortunately, the factors responsible for blooms of these algae are not well enough understood to allow precise estimates of OTEC influence on them. Based on the theory that most red tide outbreaks are associated with terrestrial runoff, they would not be expected as a consequence of OTEC operations. It is possible that minimizing disturbances of the benthic substrate (Bagnis 1981) during construction or operation of an OTEC plant will reduce the likelihood of ciguatera.

The indirect predatory effect of a 40-MWe OTEC plant on carbon or energy flow through the fishery food web is predicted to be minimal. Based on estimates of primary and secondary entrainment and impingement of various organisms by an OTEC plant (Table 7), the number of trophic transfers between the various trophic levels and fishery harvest (Ryther 1969), and an assumed trophic transfer efficiency of 15%, calculations were made of equivalent harvestable stock which would be lost due to OTEC operation. If all the entrained or impinged biomass were removed from the system, then 1.8 to 3.1 fewer kg of carbon would be available as fish harvest each day. Based on a carbon-to-live-weight ratio of 1:10, about 18 to 31 kg of fishery harvest would be lost daily. This probably overestimates actual loss because it is likely that many of the organisms killed will be eaten and thus not be lost from the food web.

Our projection that food chain effects will not significantly impact the fishery does not address direct effects on the harvested species. Many of the fishes are currently being harvested at levels equal to or greater than the Maximum Sustainable Yield (MSY). If such assessment of harvest levels is accurate, then those stocks may not be able to compensate for the individuals lost through entrainment or impingement, and yield will be reduced. Unfortunately, we do not know the fine-scale temporal and spatial distribution of the early life stages of the major species, and thus are unable to predict the number which may be impacted by OTEC operation. In addition, our knowledge of the survival of these early stages is too incomplete to predict the amount of impact on the resource.

Potential Impact on Fisheries

Defining in detail what constitutes significant adverse impact on fisheries is very subjective. Effects which reduce commercial and recreational fisheries harvest would likely be considered adverse. On the other hand, if the plant were to serve as a fish aggregating phenomenon, harvest efficiency may be increased and the overall effect considered beneficial. However, this potential beneficial effect would have to be weighed against the overall negative effect that aggregation (see Attraction/Avoidance section) may have on entrainment and impingement.

In predicting impacts of conventional power plant operations on fish population levels, scientists have relied on life cycle models which focus on those components of the life cycle which are susceptible to power plant effects at the appropriate stages. Simple models take a gross view of the life cycle, examine the environment in which the species exist, and incorporate details of the plant operations and effects. More complex models account for increased temporal resolution, more detailed environmental variation, and knowledge of behavioral responses to changes in the environment.

Table 7.—Estimated loss of living carbon and equivalent harvestable stock due to entrainment and impingement during operation of a 40-MWe OTEC plant (kg C/d). (Based on Peters 1983).

	Phytoplankton	Microzooplankton	Macrozooplankton	Micronekton
Entrainment				
Primary	100 - 170	10 - 17	12 - 21	—
Secondary	800 - 1360	80 -136	80 - 136	
Impingement	—	—	—	6 - 10
Total	900 - 1530	90 -153	92 - 157	6 - 10
Trophic transfers	5	4	2.5	1
Transfer efficiency	0.15			
Equivalent harvestable stock	0.07 - 0.12	0.05-0.08	0.80-1.4	0.90-1.5

With OTEC, adverse impacts cannot be examined with any degree of confidence because what information is available on fish eggs and larvae at potential sites is not sufficiently precise. Furthermore, effects from operations of conventional power plants can hardly be extrapolated to that of an OTEC plant because of the unprecedented volume of water the latter is expected to pump and the redistribution of water properties that will occur. However, in the absence of data which can be used as input into a life cycle model, a crude evaluation of OTEC-related impacts on fisheries has been made by Matsumoto (1984) for the purpose of this study.

Based on a review of the combined effects of impingement, direct entrainment, and biocide usage to fish, Matsumoto (1984) concluded that an assumption of total mortality of all fish eggs, larvae and juveniles, directly entrained is not unreasonable. Because the eggs and larvae of most fishes caught commercially off Kahe Point are buoyant and tend to reside near or at the surface, the degree of secondary entrainment of fish eggs and larvae will be very dependent on the discharge depth of the effluent. Little is known regarding the effects of secondary entrainment; however, Matsumoto (1984) believes the effects would be minimal for deep (e.g., 100 m) discharges. More information is needed, however, on the microdistribution of fish eggs and larvae to judge whether such a conclusion would be justified for shallow discharges where the degree of secondary entrainment may be 10 to 20 times (worst case) that of direct entrainment on the warm water side. If 100% mortality is assumed for both direct and secondary entrainment, one must then ask what effect this will have on fisheries.

Off Kahe Point, the principal fisheries that would be affected by OTEC operations include six pelagic and two demersal fish groups representing 98% by weight of the area's total annual production. The pelagic forms include tunas (mainly skipjack and yellowfin tuna), billfishes (Pacific blue and striped marlin), mahimahi, wahoo, bonefish, and jacks (principally scads), where the demersal forms include goatfishes (six species) and snappers (eight species).

Based on density values of tuna and billfish larvae at depths near the warm water intake and discharge points, and warm and cold water intake rates of 160 m^3/s (i.e., 4 $m^3 \cdot s^{-1} \cdot MWe^{-1}$), Matsumoto (1984) has estimated the extent of damage from the planned Ocean Thermal Corporation plant at Kahe Point. Assuming total mortality during entrainment, it was estimated 13.7 million skipjack and 5.5 million yellowfin larvae will be killed each spawning season. To be more realistic, these mortality figures must be adjusted for natural mortality which is estimated at 93% for skipjack and 91% for yellowfin. This would result in estimates of OTEC-induced mortality of 1.0 million and 0.5 million, respectively. Any effects of secondary entrainment would add to these figures; however, Matsumoto suspects that the effects of secondary entrainment would be minimal.

The OTEC plant is also expected to function as a fish aggregating device and attract fish from adjacent areas. Any increase of large aggregations of fishes, such as tunas, mahimahi, mackerels, and carangids, will eventually result in concentrated spawnings around the plant, subjecting more than the usual amounts of eggs and larvae to entrainment effects.

The impact on fisheries will be largely through the recruitment process. Through recruitment, the impact on pelagic species, particularly tunas, is not expected to be noticeable because most of them are migrants from the eastern Pacific fishery, the northwestern Pacific, and from equatorial waters. The effects of recruitment on bottom and reef-associated fishes would most likely be felt in areas further downstream from the plant site. If the prevailing currents carry the eggs and larvae along the coast and out into open ocean, the full impact of the damages caused by the plant may not be apparent at the plant site.

Direct effects could occur, however, in the demersal fishery. For the Ocean Thermal Corporation OTEC design for Kahe Point, Oahu (see Application section), warm effluent from the Hawaiian Electric conventional powerplant at Kahe Point is used as a supplementary heat source, and sand particles which are contained in this effluent (McCain 1977; Coles 1980) will eventually be discharged over the escarpment and build up over a period of time, blanketing the rocky bottom near the discharge point. The effect would be to force fishes such as snappers to relocate to other areas. The net effect to the fishery should be negligible, however, since demersal species comprise only a small portion (1.3%) of the total fish production off Kahe Point.

Turning to Puerto Rico, we find that the principal fisheries off Punta Tuna include four demersal and one pelagic fish groups representing 72% of the fish taken along the eastern coastline. The demersal group includes groupers (14 species), grunts (11 species), snappers (14 species), and porgies (3 species); the pelagic group is comprised of mackerels (2 species). Other pelagic fishes, such as tunas, marlins, dolphins, and jacks, comprise 1.8% of the total fish production and are caught in small numbers.

The potential effects of OTEC plant operations on pelagic fishes off Punta Tuna are also believed by Matsumoto (1984) to be insignificant. The effects there on demersal and reef fishes, however, cannot be estimated in the absence of appropriate data and biological information.

MEASURES TO REDUCE POTENTIAL EFFECTS TO FISHERIES

From the previous chapter and background reports, one can conclude that there will remain some level of uncertainty regarding the potential risk to fisheries due to construction and operation of an OTEC plant until a full-scale OTEC operation can be monitored for some period of time. However, certain aspects of an OTEC operation warrant enough concern to examine measures that would minimize the risk to fisheries of early plant operations.

First, from the viewpoint of general environmental risk, proper siting is the single most effective means to minimize the potential for environmental damage. The avoidance of areas of high biological productivity and others of special biological importance (e.g., critical habitats, spawning grounds, coral reefs) is desirable. However, the flexibility in choice of location may be limited in many of the islands that have a suitable thermal resource. For instance, as noted by Uchida (1983), there are a number of sites in Hawaiian waters that satisfy criteria for both nearshore floating and shore-based OTEC power plants. However, on the island of Oahu, only the area along the Waianae coast from Barbers Point to Kaena Point was concluded to meet certain criteria for OTEC siting (Shupe 1982). Along or offshore of this part of the Oahu coast are major coral formations and important commercial and recreational fisheries.

Once the location has been tentatively chosen, preliminary oceanographic information will have to be collected to identify initial engineering flexibility. This will include information on the thermal resource, waves and tides, currents, and extreme oceanographic events.

The power produced, and thus the cost-effectiveness of a plant, is highly dependent upon the thermal resource (ΔT). For an island plant, the site selected will therefore have to offer a suitable thermal resource within a reasonable distance of shore. One of the major trade-offs for the conceptual design by Ocean Thermal Corporation for Kahe Point, Oahu, Hawaii (Ocean Thermal Corporation 1983), was the distance offshore for placement of their "artificial island" system. The artificial island would require greater structural and construction costs in deeper waters; however greater distances offshore also reduce the cost of the cold water pipe (i.e., less length) required to achieve a certain ΔT. Greater distances offshore also reduce the cost of effluent pipes. The study conducted by OTC indicated that a plant in about 15 m of water was optimal for their design.

Assuming normal operation of an OTEC plant at a suitable location, the most important design features for which there is some flexibility to reduce the potential threat to fisheries are the cold water intake, warm water intake, discharge, and chemical additions. These topics are discussed in the following sections.

Cold Water Intake

Generally, reviews by Hoss and Peters (1983) and Uchida (1983) reveal that the direct environmental implications of the deep water intake of cold water are small. The depths involved are below the euphotic zone, estimated to be in the range of 100-150 m in subtropical waters of the Caribbean and the Pacific. As a consequence, the entrainment of phytoplankton by the cold water pipe (CWP) is not a concern.

The information on zooplankton distributions indicated that the CWP will entrain certain zooplankton. It is also apparent that the deeper the placement of the CWP intake, the fewer the number of zooplankton that will be entrained. If the CWP intake could be placed beneath the zone within which certain zooplankton undergo diel migrations (see Zooplankton section), this would also help to minimize entrainment. However, the extension of the CWP to depths deeper than necessary to achieve the needed ΔT would be very expensive, since this is one area where present technology is being advanced. This could also totally upset the financial aspects of a plant since the CWP construction and deployment costs will comprise a major percentage of the total construction and deployment costs.

It might be argued that the cost of extending the CWP to deeper depths to achieve less entrainment of zooplankton would be offset by a decrease in seawater volume requirements, and thus pumping requirements, if a sufficiently greater ΔT was obtained. Although such trade-offs will have to be examined on a site-specific basis, such factors tend to balance out when consideration is given to other factors such as the increase in pipe frictional losses. Any extension of the CWP is going to be expensive. Furthermore, although deep zooplankton play a role in the food web and thus fisheries, it is not a well defined role as yet. Therefore, the true benefit of trying to avoid deep zooplankton entrainment cannot be quantified with the present state of knowledge.

As noted by Hoss et al. (1983) and in the section on Eggs and Larvae of Important Species, little information is available on the vertical distribution of fish eggs and larvae in the Caribbean and Pacific. However, it appears that they are most abundant in the upper 25 m, particularly at night. Although Miller (1979) suggests there may be a deep source of certain larvae in waters nearshore Kahe Point, few larvae are found below 200 m. The relative lack of information on fish larvae suggests that additional information should be gathered at specific OTEC sites when a design is contemplated.

The most significant environmental implication of the CWP intake would appear to be related to the intake in these deep waters of nutrients and other natural chemical constituents, which are generally present in greater concentrations here than in surface waters (NOAA 1981a). Since the potential environmental impact does not relate to the intake as much as to the discharge of these constituents back to the ocean near the surface, this topic is taken up under discharges (see Discharge Location and Configuration).

To conclude this section, it is suggested that for most situations the placement and configuration of the CWP will be driven by economic considerations. However, the lack of flexibility in design does not seem to imply any significant disadvantage in terms of potential environmental impact and risk to fisheries.

Warm Water Intake

As discussed under Biological Interaction with the Environment, the warm water intake will have significant interaction with the biological environment, entraining or impinging phytoplankton, zooplankton, ichthyoplankton, and fish.

Generally (see Phytoplankton), the concentration of phytoplankton increases near tropical and subtropical islands due both to the upwelling of nutrients from depths as well as a greater input of nutrients from the land mass. Also, in both the Caribbean and Pacific areas under discussion, the levels of maximum phytoplankton biomass tend to be near the 100-m level, near the bottom of the mixed layer. For instance, for waters off Keahole Point, Hawaii, Noda et al. (1980) reported that the subsurface chlorophyll maximum occurred between 64 and 94 m. Chlorophyll-*a* levels tended to be relatively constant in the top 40 m or so of the water column. In general, they increase below this level to the levels found at the chlorophyll maximum and then quickly decrease to very low values, with the lowest values occurring beneath the euphotic zone. As noted by Uchida (1983) for six cruises in the Kahe Point environment, Noda et al. (1981a) observed that the chlorophyll maximum remained relatively constant in its vertical position at 86 m as well as in its concentration. Furthermore, this layer accounted for 77% of the chorophyll biomass in the photic zone.

The discussion in the section Impacts on Fishery Food Chains suggests that the predatory effect on harvestable fish stock caused by any food chain effect of the entrainment of phytoplankton is not a concern. However, where the design flexibility exists, it is probably prudent to avoid the direct entrainment of phytoplankton to the extent practicable. In light of the information on phytoplankton distributions, this would suggest that the warm water intake of an OTEC plant should probably be located in shallow water (i.e., 0-40 m). The secondary entrainment of phytoplankton is a separate issue and is discussed under the next section.

As discussed in the Zooplankton section, the abundance of zooplankton tends to be greatest near the level of the chlorophyll maximum, particularly at night when many zooplankters migrate from both deeper and shallower waters to this level. Thus, the avoidance of zooplankton to the extent practicable also suggests relatively shallow warm-water intake depths. However, as in the case of phytoplankton, the effect on fish stocks due to the predation of zooplankton by an OTEC plant of 40-MWe capacity is not expected to be significant (see Impacts on Fishery Food Chains).

Like phytoplankton, zooplankton also exhibit an island mass effect with concentrations higher at nearshore locations (see Zooplankton section). However, as evident in Table 8 for Caribbean waters, the gradient in surface zooplankton concentration is not great enough to warrant the extension, for a land-based plant.

Table 8.—Mean displacement volume, dry weight, and abundance of surface zooplankton at island sites in the Caribbean. All samples were taken with 203 μm or 239 μm mesh nets (from Hoss et al. 1983).

Location	Distance offshore (km)	Water depth (m)	Displacement volume (ml/m^3)	Dry weight (mg/m^3)	Abundance (no./m^3)	Source
Puerto Rico	0.5-1.0	10	0.086	—	818	Youngbluth 1979
Barbados	<1	10	0.049	4.00	—	Sander and Steven 1973
Barbados	2	25	0.041	3.05	345	Moore and Sander 1976
Barbados	10	460	0.028	2.40	368	Sander and Steven 1973 Moore and Sander 1977
Jamaica	1	35	0.043	8.28	1600	Moore 1967
Jamaica	8	900	0.021	3.30	823	Moore 1967

of a warm water intake to waters, say, 10 km offshore. For instance, the data suggest that the entrainment of zooplankton might be halved for an extension of the intake from less than 1 km to, say, 10 km. However, the suggestion of an insignificant effect of zooplankton entrainment on fisheries would not justify the benefit of this entrainment reduction, if indeed it was to be realized. On the other hand, if there was some flexibility over the location of the plant, e.g., whether it could be land-based or a shelf-sitter, the shelf-sitter with its location and intake being further offshore might imply a lower environmental risk on qualitative grounds, other factors being equal.

The only conclusion which can be drawn from observations of larval fish (see Eggs and Larvae section) is that the actual distributions may be quite complex. The implication is that the spatial/temporal and species distribution of larval fish should be determined before engineering flexibility in the location of the warm water intake is considered.

From the standpoint of impingement and entrainment of adult fish, the warm-water intake velocity is a critical factor with lower velocities being more desirable (see Impingement section). The general guideline regarding velocities for conventional power plant intakes is to keep the velocity below 15 cm/s so as to allow fish to escape the screen wells (U.S. Environmental Protection Agency 1973). Although the effectiveness of velocity caps (covers used to create horizontal velocity fields for a vertical intake) to reduce fish entrainment is not universally accepted, EPA recommends their use for offshore, submerged intakes; the principle is that fish tend to avoid horizontal velocity fields more so than vertical ones (see Impingement section).

Discharge Location and Configuration

The discharge of effluent waters from an OTEC operation has important implications for both the operation of the plant and its environmental effect. It is of great importance that discharge waters not recirculate to the warm water intake and thereby reduce the effective thermal resource of the plant. However, for most situations the negative buoyancy of the discharge plume and the initial dilutions achieved (see Effluent Discharge section) should assure that recirculation is not a problem. It is also of great importance that a discharge scheme be chosen so as to minimize the potential effects to fisheries and other biological resources. As discussed, the initial and, to a certain extent, subsequent fates of the effluent plume will be very dependent upon the density of the discharge, the configuration of the discharge outlet, the vertical ambient density distribution, and the presence of currents.

Several discharge situations were examined in the Effluent Discharge section: separate and mixed discharges from a 40-MWe OTEC plant to two water types that are representative of situations found offshore of Kahe Point, Oahu, and Punta Tuna, Puerto Rico. Discharges at depths of 20 m and 100 m were considered for both situations.

For the Kahe Point case considered, the upper 50 m were fairly mixed so that there was little stratification in density. The calculations showed that there would be little impedance to the sinking of effluent plumes, whether mixed or separate, until a depth of 50-100 m was reached. Discharges at 100 m did not stray too far from that depth because of the stronger stratification there. Calculated dilutions were in the range of 4-7.

The Punta Tuna case was somewhat different because of the stronger density stratification present. A separate warm water discharge at 20 m fell to 30 m, achieving a dilution of about 4; whereas a separate cold water discharge fell further, to 55 m with a dilution of 5.5. A separate warm water discharge at 100 m rose, because of its positive buoyancy at that depth, to 75 m with a dilution of 5; the separate cold water discharge at 100 m fell to 160 m with a dilution of 7. A mixed discharge at the 20-m depth fell 25 m to a depth of 45 m with a dilution of 4.5, and a mixed discharge at 100 m fell 15 m to 115 m with a dilution of 5.

Although the examples offered are limited, they do provide an indication as to how the level of neutral buoyancy (where the density of the plume equals that of the ambient waters) and dilutions are affected by the type of discharge. For a given situation, larger differences in density between the discharge and receiving waters will involve longer trajectories and higher dilutions before a neutral buoyancy is achieved. This may be desirable if dilution and removal of certain constituents (e.g., chlorine) from the immediate environment is desired. However, it might be undesirable if the redistribution of organisms is a concern, or if the utilization of nutrients from the cold water is possible and desired. Long trajectories and high dilutions also result in larger secondary entrainment of the organisms which could have an effect many times that of primary entrainment.

This brief treatment of discharge schemes provides only a glimpse of the discharge possibilities and how they might be used to advantage. The presence of currents, occurrence of coastal upwelling, and placement of the plant will greatly influence the final schemes chosen. Also if the plant is land-based, an artificial island, or a shelf sitter, the presence of the seabed may influence the selection. For example, a mixed effluent discharged to shallow waters will probably hit the seabed before it reaches its level of neutral buoyancy. This would affect the rate of subsequent dilution and also cause impact to benthic biological resources in the area, such as corals. It is obvious that the discharge scheme, more so than either of the intakes, will have to be fine-tuned to the environmental conditions at a site.

Chemical Additions

Chemicals will be added to the seawater pumped through an OTEC plant by the corrosion/erosion of heat exchanger surfaces, the addition of biocides to control the biofouling of heat exchanger surfaces, and the leaking of working fluids. The release rates will be determined by both the engineering design and the biological-chemical characteristics of the local ambient waters. For the most part, the normal release of working fluids and metals from heat exchanger and other surfaces is not expected to be a problem (see Chemical Additions section).

Given that a biocide such as chlorine may be a necessary evil for an OTEC operation, a certain amount of engineering flexibility can still be utilized to reduce the degree or scale of potential effects. All of the previously discussed options are definite candidates (i.e., plant location and intake/discharge schemes). For instance, achieving a high dilution and a level of neutral buoyancy below the euphotic zone may be very desirable to limit the exposure of biota to the biocide. This would require the identification of a certain optimal discharge scheme. In addition, certain dosing schemes can be used.

Flexibility in biocide dosing might involve applying the biocide to different power modules at different times and mixing the dosed module effluent with other module effluents to create some degree of pre-dilution. For instance, if a 40-MWe OTEC plant was composed of four 10-MWe modules and the condenser and evaporator could be dosed separately, a certain dose to one of the evaporator units and subsequent mixing with the total warm and cold water discharge would produce a dilution of 8 to 1 prior to discharge. In other words, a free residual chlorine level of 0.05 μg/g in the effluent of the evaporator or unit in question would be diluted to 0.006 μg/g before discharge to the environment. Initial dilutions of 5 to 10 could further reduce these concentrations to 0.0012 and 0.0006 μg/g, respectively.

RESEARCH PRIORITIES

The preceding sections have presented information and inferences regarding the potential effects of OTEC operations on fisheries. The discussions have primarily relied upon information on power plant effects in temperate waters and the limited biological information available for tropical waters. Although such an assessment provides valuable insights regarding the effects of early small-scale OTEC development, a more thorough assessment will eventually be needed. To do so will require much additional research of both generic and site-specific types as defined below. However, although further research is needed, the preceding sections also allude to areas where additional information is either not needed or deemed to be unimportant. Specifically, the assessments in the Biological Interactions section of the predatory effect of an OTEC plant on phytoplankton and zooplankton (with the exception of ichthyoplankton) would suggest that the effect is so minimal as to not warrant further investigation of this topic. As emphasized below, additional information on the eggs and larvae of fish is direly needed.

Investigations of Fish Distribution

There is almost no quantitative information available on the distribution of the early life stages (eggs to juveniles) of fish in tropical waters. Both spatial and temporal information of this type is needed and should be given high priority, in order to determine the potential numbers of fish that will be subjected to impingement and primary and secondary entrainment. An understanding of the distribution of fish in the water column may allow plant modifications to be made that will help decrease the environmental impact of OTEC operations.

Studies on the Effects of Entrainment

Primary and secondary entrainment effects associated with OTEC are potentially important because of the extremely large volumes of water involved. Unlike conventional power plants where organisms experience an increase in temperature as they pass through the condensers, larval fish entrained in an OTEC plant will be subjected to a decrease in temperature of about 2°C upon passage through the evaporators. Additionally, in the case of a mixed discharge, organisms entrained in the warm water intake will be further subjected to a decrease in temperature of about 10°C when the warm and cold waters are mixed. Depending on where this discharge is made, secondary entrainment may expose additional organisms to some temperature decreases.

Since we found no reported work on the effects of cold shock on the young of tropical fish, research on this subject was initiated by the National Marine Fisheries Service. This research is examining the effects of cold shock (using realistic decreases in temperature) that could occur as a result of entrainment. In the future, factors such as the addition of biocides and increased levels of trace metals in the water should be examined in conjunction with the temperature studies.

Biostimulation/Inhibition

The OTEC plants are unique in their utilization of cold water from the deep ocean. This use of large amounts of deep ocean water creates a potential for changes in the upper part of the water column similar to those caused by natural upwelling. The increased nutrient load of cold, deep ocean waters may have stimulating, inhibiting, or no effects on the productivity of marine fisheries.

Although some experiments have described the effect of mixing deep water with surface waters at potential OTEC sites (e.g., Quinby-Hunt 1979; Szyper et al. 1984), further work is needed. This research should look at nutrient and trace metal distributions of waters from different depths and test their ability to affect primary production and species composition. This type of research can be completed in a relatively short time, and the results must then be combined with the effects of natural nutrient fluxes to determine the ecological significance of potential changes in primary production.

Early Life History Studies

It appears that the major direct impacts of OTEC operations on fish will be on the early stages in their life history. In order to evaluate OTEC impacts on these stages, we need more information on their abundance, distribution, migration, and growth and mortality rates. Generic information on tropical species is lacking and general principles may be applicable to many species. Such information should be collected, starting with some of the major recreational and commercial species. The duration for this type of research is in years, but specific parts can be completed in less time.

Dynamics of Fishery Populations

The research priorities outlined above are directed at establishing the effects of OTEC operations on the biological community which supports and includes harvested fishery populations. Such research should indicate whether effects may be positive or negative and supply information needed to predict the number and life stage of fish directly impacted. In order to evaluate any such effects as they relate to commercial or recreational fisheries, additional information is needed. For example, while some information is available on many of the fisheries, much more is needed, including:

1) Stock structure (i.e., the number and geographic distribution of the stocks);

2) stock assessment over time, which depends upon age distribution of the stocks, size at age, and age-specific fecundity,

3) accurate catch and effort statistics, and

4) increased information about the factors affecting recruitment, including development of models to predict compensation for mortality at various early life stages.

Although parts of this research area can be performed over short time scales, the topic as a whole will require years to address adequately.

Ciguatera

Independent of other impacts, fisheries could be severely impacted if the fish present were inedible due to ciguatera fish poisoning, which occurs in many tropical waters. Current information is inadequate to predict or prevent such an occurrence, and additional information is needed, including a description of the environmental factors responsible for blooms of the toxin-producing algae, methods of easily detecting contaminated fish, and methods of mitigation.

Construction Effects

Further research is also needed to properly assess the effects from disturbances to the environment (including the fisheries) by actual construction of the OTEC facility. Any dredging in open seas will generate turbidity and sedimentation, not only in the immediate area of construction but also in adjacent areas. Sediment in the dredging plume will settle out of the water column, covering and perhaps killing some benthic life, including, possibly, coral communities. Dredging has also been found to be correlated with outbreaks of ciguatera poisoning. Thus, in addition to the information needed on ciguatera, there is a need to gather data on effects of sediments on coral reef ecosystems as well as on the downstream extent of the dredging plume.

CONCLUSIONS

This report examines the potential impact to fisheries due to the operation of ocean thermal energy conversion (OTEC) plants. The effort is primarily a synthesis of existing information that has pertinence to the topic, and an extrapolation to conditions brought about by OTEC operations. The intent was to gain a perspective of the potential risk to fisheries, to identify practicable measures that would reduce the potential for problems, and to suggest research areas where significant uncertainties exist, uncertainties that under certain conditions might impede the commercial development of OTEC.

The report focused on two regions where U.S. OTEC interests might lie: the Caribbean and the Pacific. It also focused on nearshore operation of OTEC as compared to open ocean application; the rationale here is that the nearshore area is considered to be the more ecologically sensitive as well as more likely to see OTEC development in the near term. Additionally, the report has contained itself primarily to those factors of concern that would be associated with the normal operating conditions of an OTEC plant: the impingement and direct entrainment of biota, the secondary entrainment of biota, the redistribution of ocean water properties, and the addition of biocides and other chemical constituents. These concerns are highlighted by the relatively large volume of water that will be pumped through OTEC plants.

Fish impingement rates caused by these flows will depend on the abundance of fish which are larger than the mesh size of an OTEC intake screen and on the ability of the fish to avoid the intake. Although this avoidance ability will also depend on a number of factors, it can be increased through the use or creation of horizontal intake flow fields. It can also be increased by keeping the flow speeds as low as practicable. It is estimated that a 40-MWe Hawaiian or Puerto Rican OTEC plant would impinge about 20-35 kg of organisms daily, due to the warm water intake, and another 40-65 kg at the cold water intake. It is estimated that the effect on a fishery of such impingement rates will be negligible compared to other pressures on a fishery; however, the use of the above mitigating measures and attempts to locate intakes away from areas of high biological activity are recommended.

Organisms, including fish eggs and larvae, that are caught up in the intake flows and not impinged, will be entrained, travel through the plant, and then be discharged. Although the combined effect of the various stresses that these entrained organisms would undergo is difficult to quantify with accuracy, it is considered prudent to assume 100% mortality until better knowledge is available. Additionally, entrainment mortality will be added to by the secondary entrainment of organisms. This entrainment is due to a discharge plume that, in falling or rising to find its level of neutral buoyancy, entrains surrounding water and biota as it is diluted. With typical dilution ratios expected to be in the range of 5:1 to 10:1, the level of secondary entrainment may be quite high. However, until further information is gathered, assessments of the associated mortality are very subjective. It is concluded that cold shock to biota may be the main concern with secondary entrainment and that organisms may only suffer slightly. However, the most vulnerable of the organisms will be the non-migratory species; and these, unfortunately, include many larvae.

OTEC plants have the potential of influencing the food chains leading to fish in several ways. Increased fish production can occur through either more primary production or shorter food chains, either of which could result from the "pumped upwelling" of nutrient-rich deep water. On the other hand, minor changes in food webs may drastically alter our acceptance of the fish produced. For example, blooms of the dinoflagellates which cause red tides or ciguatera can make the fish inedible. Although more information is needed on such processes, red tide outbreaks are not expected and the minimization of benthic disturbances during OTEC construction and operation will reduce the likelihood of ciguatera outbreaks.

In trying to examine impacts to fisheries due to mortalities associated with OTEC operations, one key problem is the lack of detailed information on the spatial and temporal distribution of fish eggs and larvae, the natural mortality of most fish, and the range of natural variability associated with the various life stages of fish.

This results in a low degree of confidence in anything beyond rather subjective conclusions. However, even these conclusions are valuable until further information is gained.

Design measures that might be taken to reduce the potential risk to fisheries relate to the location of the plant, location and configuration of the intakes and discharges, and the mode of introducing biocides to the system. From the viewpoint of general environmental risk, proper siting is the single most effective means to minimize the potential for environmental damage. Here, the avoidance of areas of high biological productivity and of others of special importance (e.g., critical habitats, spawning grounds, coral reefs) is desirable.

For most situations the placement and configuration of the cold water pipe will be constrained purely by economic considerations. However, the perceived lack of flexibility does not seem to imply any significant disadvantage in terms of potential environmental impact and risk to fisheries. Regarding the warm water intake, it is felt that more information is needed on the microscale distribution of fish eggs and larvae. However, in general, it is believed that warm water intakes placed below the surface, where many fish eggs tend to concentrate, and above the chlorophyll maximum may be most desirable. This suggests a placement between about 10 and 40 m. Additionally, if there was some flexibility over the location of the plant, particularly its warm water intake, a plant located further offshore might imply a lower environmental and fishery risk on qualitative grounds, other factors being equal.

The placement and configuration of discharges will be a very site-specific consideration. Mixed vs. separate, and deep vs. shallow, discharges can achieve different dilutions and levels of neutral buoyancy. Different permutations have implications regarding the utilization of cold water nutrients, the potential for recirculation into the warm water intake, the degree of secondary entrainment, the amount of cold shock, and the concentration of biocides. Brief treatment of the possibilities suggests that in deeper waters the discharge of a mixed effluent near the surface would offer a number of advantages. First, the cost of the discharge structure is minimized. Second, the plume, because of the density addition provided by the mixed cold water, would probably sink deep enough to avoid problems of recirculation into the warm water intake. Third, sufficient dilution would be imparted to minimize potential problems with biocides and other trace constituents. Also, the mixed discharge would minimize the degree of cold shock to organisms secondarily entrained. However, with the discharge near the surface, there may be some impact associated with the entrainment of ambient water and organisms into the discharge plume.

The presence of currents, occurrences of coastal upwelling, and placement of the plant will also influence the final discharge scheme chosen for a particular plant. For instance, for a land-based or very nearshore plant, the effluent from a nearsurface discharge will probably hit the seabed and roll down it before the level of neutral buoyancy is reached. Depending upon a number of factors, e.g., benthic resources, this might necessitate a deep discharge.

In general, it is not believed that the effect of the corrosion products of metals will be a problem with OTEC. However, the addition of chlorine as an antifoulant over long time periods does create some concern. Although more information is needed on the chemistry and long-term effects of chlorine, this concern is lessened through the achievement of high dilutions of the biocide and/or a level of neutral buoyancy near the bottom of the euphotic zone. Certain dosing schemes can be utilized to achieve predilutions that, combined with the initial dilution process would result in much lower levels of biocides in the environment.

In conclusion, the potential risk to fisheries of OTEC operations is not judged to be so great as to not proceed with the early development of OTEC. Due to the lack of a suitable precedent, however, there will remain some level of uncertainty regarding these initial conclusions until a pilot plant operation can be monitored for some period of time. In the meantime, further research on fisheries should be undertaken to assure an acceptable level of risk regarding the larger commercial OTEC deployments.

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8673

REPRODUCTIVE BIOLOGY OF FEMALE SPOTTED DOLPHINS, *STENELLA ATTENUATA*, FROM THE EASTERN TROPICAL PACIFIC

A. C. Myrick, Jr., A. A. Hohn, J. Barlow, and
P. A. Sloan[1]

ABSTRACT

Reproductive parameters were estimated from about 4,700 female spotted dolphins collected in the eastern tropical Pacific from 1973 to 1981. From this sample, specimens for which ages were estimated were divided into two subsets and were used to estimate age-specific rates for the northern offshore stock of this species. The youngest sexually mature individual was 10 years old; the oldest immature was 17 years; the youngest and oldest pregnant individuals were 10 and 35 years, respectively. There was high individual variability in the accumulation of corpora with age; the ovulation rate appears to slow abruptly after the eighth ovulation. Average age at attainment of sexual maturity (ASM) for all years ranged from 10.7 to 12.2 years ($\bar{x}$ = 11.4 years) for two sets of age estimates; no significant temporal change in ASM was detected. Correlation between color phase and state of sexual maturity suggests that color phase may be a good indicator of maturity for this stock. The average annual pregnancy rate was about 0.33; this rate did not change significantly with age. The calving interval was 3.03 years (SE = 0.205). The lactation period was 1.66 years, but there was a significant increase noted in the percent lactating from 1973 to 1981. A low percentage of postreproductive females was found in the sample (0.4%) indicating that reproductive senescence is of little importance in reproductive rates of this stock.

Purse seine operations of the yellowfin tuna fishery in the eastern tropical Pacific Ocean (ETP) have caused high mortality of the spotted dolphin, *Stenella attenuata* (Perrin 1969a, 1970). Estimated incidental kills for the northern offshore stock of spotted dolphins were between 100,000 and 400,000 annually throughout the 1960's and early 1970's (Smith 1983). Since 1968, research efforts by the National Marine Fisheries Service (NMFS) have focused on assessing the biological consequences of the large incidental kill of this and other affected dolphins using specimens and data collected by NMFS observers aboard U.S. tuna seiners. Perrin et al. (1976) presented the first comprehensive description of spotted dolphin life history and reproduction for specimens from the ETP. The accumulation of thousands of additional specimens, the sharp decline in dolphin mortality (Smith 1983; Hammond and Tsai 1983), and the improvements made in estimating age since that study (Myrick et al. 1983) have made a new analysis necessary.

The purpose of this paper is to estimate the reproductive parameters of the female spotted dolphin, based on analyses which include more data and a better age estimating method than previous studies. Reproductive features of the male spotted dolphin (Hohn et al. 1985) and temporal trends in reproduction in the northern offshore stock (Barlow 1985) are discussed in separate papers.

MATERIALS AND METHODS

Samples

The specimens were analyzed as three samples. The "overall" sample contained about 4,700 specimens that had been collected from 1973 through 1981. A second sample for which ages were estimated contained 580 specimens selected randomly from more than 3,500 specimens collected in 1973 through most of 1978 (the 1973-78 aged sample). The randomly chosen 1973-78 aged sample did not include any of the specimens studied by Perrin et al. (1976). The third sample (the 1981 aged sample) was composed of 226 specimens which had been collected in 1981 and for which ages were estimated. It included almost all specimens for which ovaries and teeth were collected in that year. The two aged samples, referred to collectively as the aged sample, are subsets of the overall sample. In several analyses the 1973-78 aged sample was divided into 1973-74 and 1975-78 subsamples in an effort to detect possible temporal changes in reproductive rates. Only the

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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northern offshore stock of spotted dolphins (as defined by Smith 1983) is treated in this analysis. The geographic boundary used to divide it from a southern stock is lat. 1°S (Henderson et al. 1980).

Life History Data

Data and specimens were collected by biological technicians aboard tuna purse seine vessels in the ETP. Biological data used in this analysis are body length, color phase, reproductive condition (pregnant, lactating, or resting), and corpora counts for each specimen (see Perrin et al. [1976] for a description of collection and examination procedures). Although there is no certainty that all ovarian corpora persist for life in all delphinids (Perrin and Reilly 1984), corpora counts were used with age to estimate ovulation rates. Counts included corpora albicantia (CAs), corpora lutea (CLs), and in some cases corpora atretica (atretic follicles). Only specimens that had both ovaries examined were included in the ovulation rate analyses.

Age Estimates

Ages were estimated for about 800 specimens (from 1973 to 1978 and 1981 samples) by counting growth layer groups (GLGs, Perrin and Myrick 1980) in the dentine and cementum of decalcified and hematoxylin-stained thin sections (Myrick et al. 1983). Tooth readings were made independently by two readers (A. C. Myrick and A. A. Hohn), without referring to field or laboratory data on size or reproductive condition. For the 1973-78 sample, a tooth of each specimen was read at least three times by each reader. Age estimates by each reader were significantly different (Reilly et al. 1983). To minimize the differences, the mean of the multiple age estimates by each reader was calculated and the average of the two means was used as the estimate of a specimen's age. For the 1981 sample a tooth from each specimen was read once by each reader after calibration tests showed that differences in estimates between readers were acceptably small (Reilly et al. 1983). An average of these two readings was used for specimen age.

We consider the method we used to estimate ages improved over that used by Perrin et al. (1976) because

1) the preparation technique we used provides superior resolution of GLGs (Myrick et al. 1983);

2) the new method of reading utilizes GLGs in the cementum as well as in dentine and allows a more accurate estimate of maximum age for adults (Myrick et al. 1983; see also Kasuya 1976);

3) calibration of GLGs in tetracycline-labeled teeth of Hawaiian spinner dolphins, *Stenella longirostris* (Myrick et al. 1984), has provided a basis for interpreting dental layering within an absolute-time framework (Myrick et al. 1983; Myrick et al. 1984). Perrin et al. (1976) used the term tooth layers in lieu of known time units.

RESULTS AND DISCUSSION

Composition of Samples

Chi-square (contingency) tests were used to evaluate whether fractions of mature, pregnant, and lactating females in the 1973-78 aged sample were a representative subset of the overall sample for those years. For all three tests, differences were not significant ($P > 0.05$).

Reproductive statistics showed some differences between years (Table 1). Chi-square tests were carried out for homogeneity between 1973-74 and

TABLE 1.—Number of sexually mature, pregnant only, lactating only, simultaneously pregnant and lactating, and "resting" female spotted dolphins, and the proportion of the sample pregnant or lactating in the aged and overall samples. The proportion pregnant and proportion lactating include the simultaneously pregnant and lactating specimens.

	Number					Proportion	
Years	Sexually mature	Pregnant only	Lactating only	Pregnant and lacting	Resting	Pregnant	Lactating
Aged							
1973-74	188	57	87	7	38	0.34	0.50
1975-78	205	48	100	13	44	0.30	0.55
1981	149	34	86	9	17	0.29	0.64
Total	542	139	273	29	99	0.31	0.56
Aged and unaged							
1973-81	2,979	780	1,480	151	568	0.31	0.55

1981 aged samples and between 1975-78 and 1981 aged samples for numbers of specimens pregnant, lactating, and resting. These tests revealed significant differences (1973-74 vs. 1981: $\chi^2_2 = 7.46$, $P = 0.024$; 75-78 vs. 1981: $\chi^2_2 = 6.16$, $P = 0.046$.). These differences are the result of an increase in the relative frequency of lactating females (see section on Lactation Period). There were no differences in percent pregnant during this time (see also Barlow 1985).

Ovulation Rate

Individual Variability

Perrin et al. (1976) found high variability in the number of corpora (corpora atretica included) for a given age (in tooth layers). Nevertheless, by fitting a power curve to the average number of corpora as a function of average reproductive age, they determined that the average ovulation rate slowed abruptly from about "four during the first layer, [to] two during the second, and about one per layer thereafter" (Perrin et al. 1976, p. 261).

The sexually mature specimens in the combined aged samples were used in our study to plot average frequency of corpora (corpora atretica excluded) on estimated age (Fig. 1). Regressions for the 1973-74 sample and for the 1981 sample are not significantly different; when the samples are pooled, the resulting slope is 0.61 corpora/yr. A plot of number of corpora on age for all individuals ($n = 542$) in mature age classes (10 through 38 yr old) for all aged specimens (Fig. 2) showed a significant slope ($P < 0.0001$) but a low correlation ($r^2 = 0.397$), indicating high individual variability. For example, the sample included 12- and 13-yr-olds with 7 or 8 corpora, and 21-yr-olds with 4 or fewer corpora. A 38-yr-old had only 11 corpora (Table 2). These results support those of Sergeant (1962), Brodie (1971), Kasuya et al. (1974), and Perrin et al. (1976), that great individual variation occurs in ovulation rates among odontocetes.

TABLE 2.—Summary of age-related reproductive statistics for female spotted dolphins taken in 1973-78 and 1981.

Variable	Estimated age (years)
Range of ages with no corpora	0-17
Oldest with one corpus	23
Youngest with one corpus	10
Youngest pregnant	10
Oldest pregnant	35
Average age pregnant	18
Oldest simultaneously pregnant and lactating	29
Oldest lactating	36
Youngest lactating	10
Oldest	38

Changes in Rate

Ovulation rate apparently decreases with reproductive age. If ovulation and mortality rates were

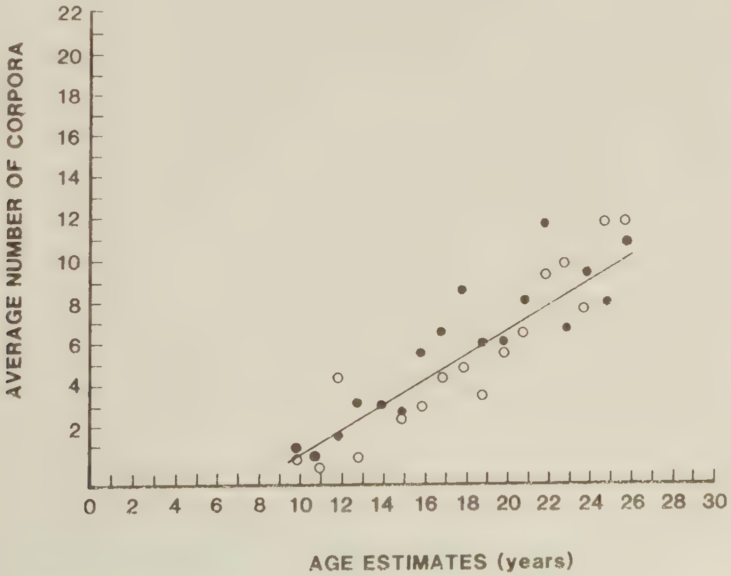

FIGURE 1.—Linear regression of number of corpora on estimated age as gross estimates of ovulation rates in female spotted dolphins. Points represent averages for 1-yr age classes (1973-78 samples = closed circles; 1981 sample = open circles).

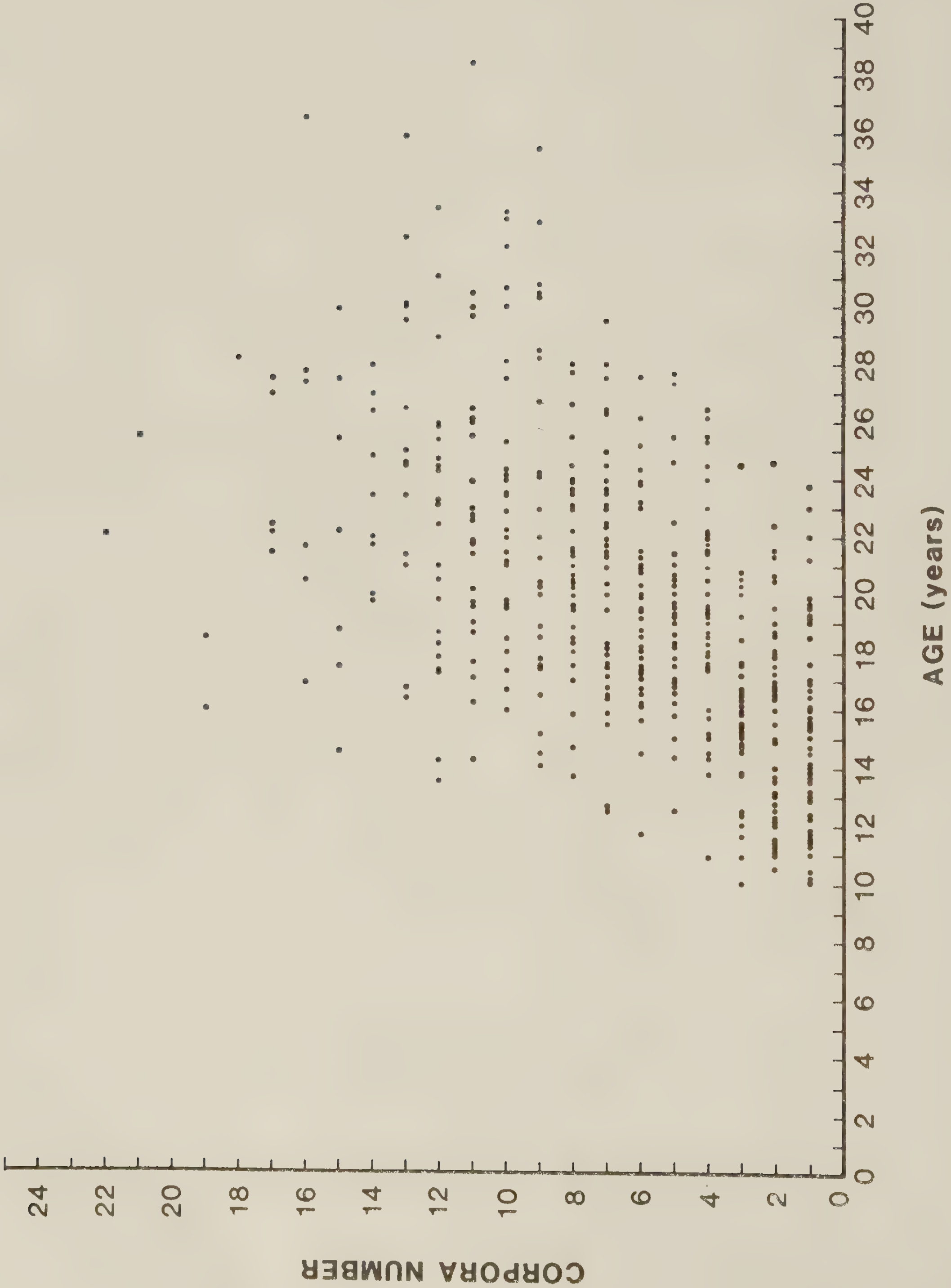

FIGURE 2.—Plot of total corpora (excluding corpora atretica) on estimated age for 542 mature female spotted dolphins collected in 1973-78 and 1981.

constant, a semilog plot of the frequency distribution of corpora counts would be linear. The slope of this line would be negative, and its value would be determined by mortality and ovulation rates. The observed shape of the log-frequency distribution of corpora counts for spotted dolphins (Fig. 3) suggests that ovulation and/or mortality rates are not constant. After about eight ovulations, log-frequencies decrease monotonically and nearly linearly. For up to the first eight ovulations, the rate is apparently much higher (presuming, again, that mortality rates do not change with the number of ovulations and that all CAs persist for life [Perrin and Reilly 1984]) This supports the findings of Perrin et al. (1976) that ovulation rates decrease with reproductive age in spotted dolphins.

Sexual Maturity

The age at which a female first ovulates is considered the age at attainment of sexual maturity (DeMaster 1978, 1984). Using the aged samples, we estimated average age at sexual maturity (ASM) using two methods. For these estimates, ages were grouped by 1-yr intervals: age-class 1 included specimens 0-1.0 yr, age-class 2 from 1.1 to 2.0 yr, etc. The mean age of sexually mature females was 18.7 yr.

Method-One

ASM was estimated from both readers' age estimates using a variation of the method described by DeMaster (1978). Age-specific maturation rates were used to calculate mean ASM as

$$\text{ASM} = \sum_{x=1}^{w} (x - 0.5)\, P_x$$

where x is age class, P_x is the probability of first ovulating in age class x, and w is the maximum age in the sample. The term $(x - 0.5)$ was substituted for DeMaster's (x) so that the mean age in an age-class interval would be represented by the midpoint of that interval. The terms P_x were estimated as

$$P_x = f(x + 1) - f(x),$$

where $f(x)$ is the probability of being mature at age x. The function $f(x)$ was estimated as the best least-squares fit of a curve (York 1983) to the observed values of percent mature by age class. A 3-parameter sigmoid curve based on a modification of the logistic equation was found to give an adequate fit of the data (Fig. 4).

ASMs were calculated separately for the aged samples, 1973-74, 1975-78, and 1981. There were no significant differences among these samples ($P > 0.05$). The ASM for all samples combined was 10.7 (var. = 0.03) to 12.2 (var. = 0.05) yr for the two readers. The average of these two ASM estimates was 11.4 yr. The precision between readers in age estimates of the 1981 specimens was greater than

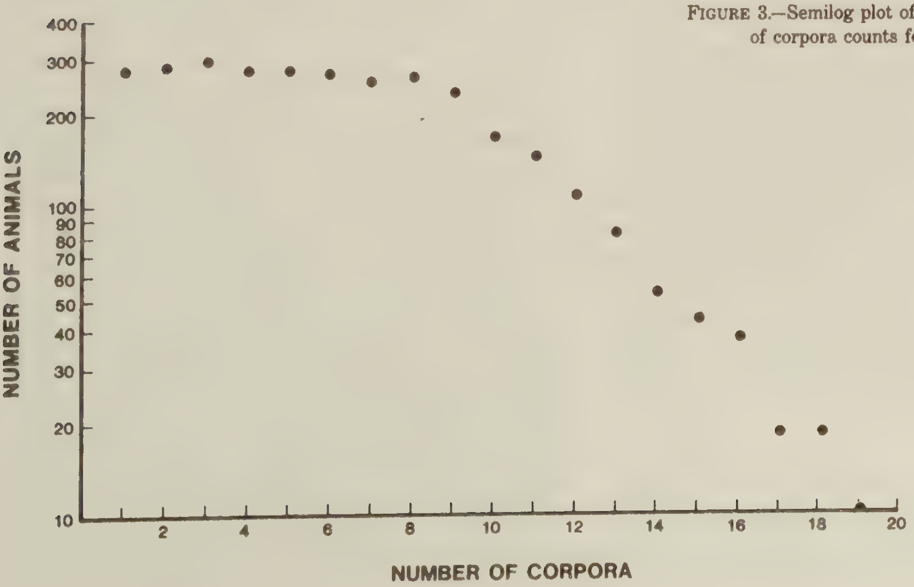

FIGURE 3.—Semilog plot of the frequency distribution of corpora counts for female spotted dolphins.

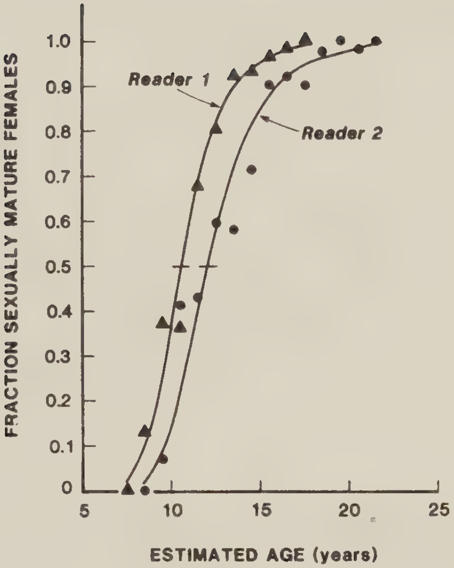

FIGURE 4.—Fraction of sexually mature female spotted dolphins versus age based on estimates of two readers. Logistic curves are fitted to the data. Bars predict ages at which 50% are sexually mature.

for the 1973-78 specimens (Reilley et al. 1983); the mean ASM range for the 1981 sample was 11.6-11.7 yr.

Method Two

The second method we used for estimating ASM was to interpolate, from a maturation curve, the age at which 50% of the specimens were mature. Again, sigmoid curve fits of the percent of mature specimens as a function of age were used for the maturation curves. For all aged samples combined, the method predicts an ASM of 10.6-12.0 yr (for the two readers), with an average of 11.3 yr.

Our overall estimates of ASM (11.3 or 11.4 yr) differ markedly from the ASM estimated for ETP spotted dolphins by Perrin et al. (1976) which was 9 tooth layers, "5.1 to 8.3 yr, depending on [which] layering hypothesis is used" (p. 250). Our estimates also differ from the ASM estimate for spotted dolphins off the Japanese coast by Kasuya (1976) which was 9 yr.

Biases in ASM

All of the above estimates of ASM are dependent on two important assumptions. First, we assume that counts of dentinal and cemental GLGs give precise and unbiased estimates of age. Second, we assume that our samples are unbiased with respect to the maturity of the specimens collected. Potential biases would result if the assumptions were invalid. Because age estimates of the two readers differ significantly (Reilly et al. 1983), the difference in ASM estimates for the readers (1.5 yr) should be taken as a minimum range in the ASM estimates.

Color Pattern and Maturity

Perrin (1969b) described the ontogenetic development of color pattern in spotted dolphins in the ETP: he divided the development into five sequential phases (neonatal, two-tone, speckled, mottled, and fused) based on patterns of ventral and dorsal spots. Kasuya et al. (1974) described color-phase changes in western Pacific spotted dolphins using somewhat different definitions than those of Perrin (1969b), although the description indicated that the ontogenetic changes were similar to those observed by Perrin. Perrin (1969b) found a close correlation between size and color pattern and (for a smaller sample) between sexual maturity and color pattern. Kasuya et al. (1974) found that the development of the adult color pattern in spotted dolphins from the western Pacific coincides with the attainment of sexual maturity.

In our sample of spotted dolphins, there was considerable overlap in age and length between animals with different color patterns, but a correlation between color pattern and state of maturity was evident. In females from the aged sample, speckled animals ranged from 3 to 18 yr, mottled from 6 to 32 yr, and fused from 10 to 38 yr. A similar overlap occurred in body-length distribution from the overall sample of females, 135-200 cm (n = 166), 140-210 cm (n = 179), and 155-220 cm (n = 188) for speckled, mottled, and fused specimens, respectively. However, 96% of fused animals (n = 2,764), 50% of mottled animals (n = 857), and only 4% of speckled animals (n = 559) were sexually mature.

In addition, for a given length or age class, females with a fused color pattern appeared to have been mature for a longer time than animals with a mottled pattern. For females of similar lengths, mature specimens with a fused color pattern had more corpora than those with a mottled color pattern (Fig. 5). Similarly for the aged sample, the fused specimens within a given length group tended to have more total corpora than mottled specimens, and when specimens in the same body length categories were of similar ages, fused animals had more total corpora.

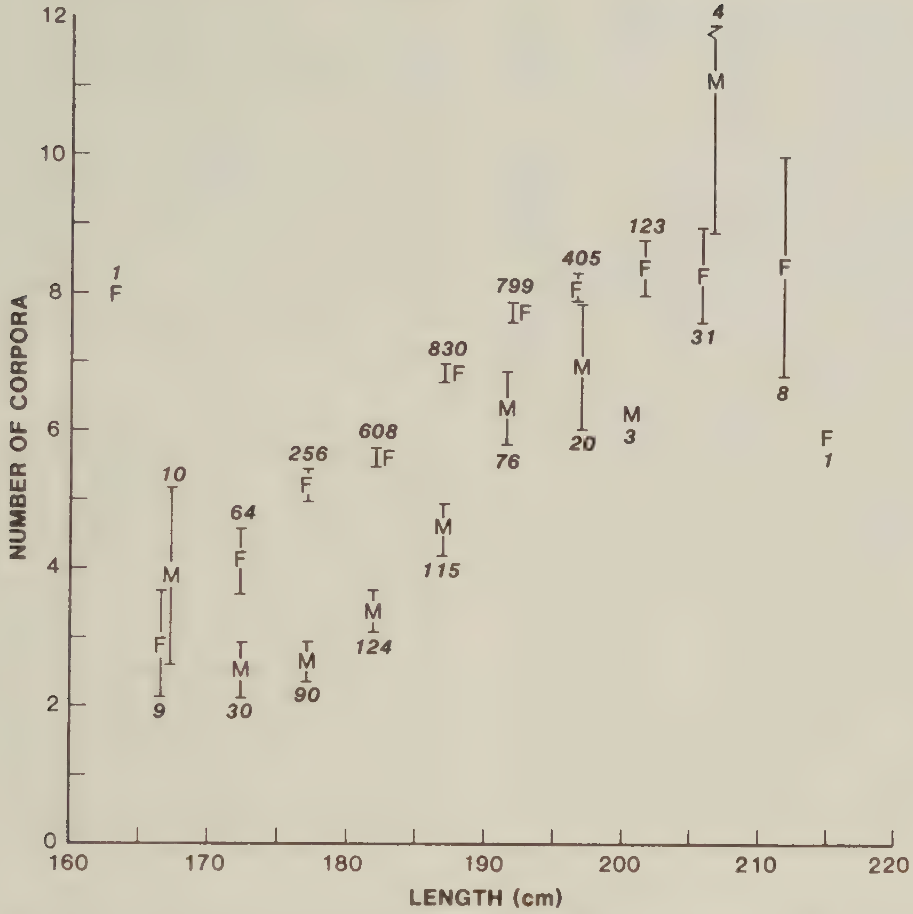

FIGURE 5.—Average number of corpora for mottled (M) and fused (F) color-phase specimens within each 5 cm length grouping for the overall sample of female spotted dolphins. Bars represent one standard error from the mean. Sample sizes are shown.

These results suggest that color phase may indicate sexual maturity more accurately than either age or length. Perrin (1969b) found 0% speckled ($n = 5$), 60% mottled ($n = 16$), and 100% fused ($n = 33$) females to be sexually mature. Using color phases that roughly correspond to the late mottled and fused stages of Perrin (1969b), Kasuya et al. (1974) found that 93% ($n = 30$) of the spotted dolphins in the third stage and 100% in the last (fourth) stage of dorsal spotting were sexually mature. A similar relationship between maturity and color pattern exists in male spotted dolphins in the ETP (Hohn et al. 1985). Assuming that the proportion of mature specimens in a given color phase does not change within a population, it would be possible to estimate the percentage of sexually mature specimens in a sample without having to examine the ovaries for corpora.

Pregnancy Rate

The annual pregnancy rate (APR) of a population is the fraction of mature females that would be expected to give birth in any given year. APR can be estimated as the average fraction of mature females that are pregnant divided by the gestation time in years. The variance of this estimate is approximated by

$$\text{var(APR)} = (-P/T_{G^2})^2 \text{ var } (T_G) + (1/T_{G^2})\, P(1 - P)/n_p$$

where P is the proportion pregnant, T_G is the gestation time, and n_p is the sample size used to estimate P (Perrin and Reilly 1984). We use 0.958 yr (11.5 mo) as the gestation period for spotted dolphins (Perrin et al. 1976). The variance in gestation time has not been calculated. We can, however, reasonably estimate that 95% confidence limits would span 0.1 yr. From this we estimate the var (T_G) to be 0.000625.

For the aged sample, 31.1% of the sexually mature specimens ($n = 542$) were pregnant. For the overall sample during the same years, 31.6% of the sexually mature specimens ($n = 2{,}458$) were pregnant and for all aged and unaged mature specimens from 1973 through 1981 inclusive ($n = 2{,}979$), 31.3% were pregnant (Table 1). By dividing the fraction of pregnant females by the gestation period (0.958), annual pregnancy rates of 0.325 and 0.330 were obtained for the aged and overall samples, respectively. The var(APR) for the overall sample is 0.0005.

To determine whether pregnancy rates changed with age, we estimated percent pregnant for four age-class intervals using the 1973-78 and 1981 samples combined. Sample size was small for estimating age-specific rates with much precision. Nevertheless, we detected neither a sustained increase nor a sustained decrease in the percent of pregnant females with age (Fig. 6); the variability in the percent of pregnant females with age can be accounted for by random sampling ($\chi^2_3 = 4.6$, $P > 0.50$). This result differs from that of Perrin et al. (1976) which indicated a significant reduction in pregnancy rate with age.

Calving Interval

Calving interval is an estimate of the mean period between births for mature females. Typically, it is estimated as the inverse of the annual pregnancy rate (Perrin and Reilly 1984). The principal requirements for calculating the calving interval are unbiased estimates of gestation time and of the fraction of mature females that are pregnant. The standard error in an estimate of calving interval (CI) by these methods is approximated by

$$\text{SE (CI)} = (\text{APR-4})\ \text{var(APR)}$$

(Perrin and Reilly 1984).

Given our calculated APR estimate of 0.330 for the overall sample, the calving interval is 3.03 yr. The standard error of this estimate is about 0.205. Although it is difficult to prove that our estimates of the percent of pregnant females are unbiased, support for such a position is given by Barlow's finding that the percent of pregnant females varies little with sampling conditions (including sampling season, geographic area, dolphin school size, and dolphin kill-per-set) (Barlow 1985). However, if annual variability in the percent of pregnant females is important, binomial sampling theory is likely to underestimate our certainty in estimating the percent of pregnant females, APR, and calving interval. Because no significant trends were detected in the percentage

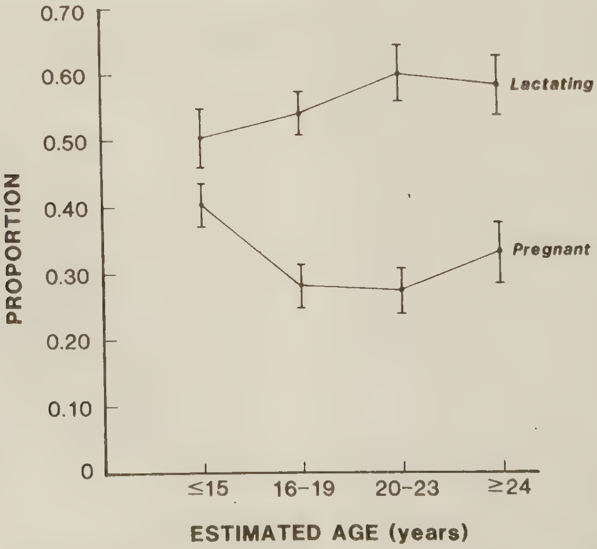

FIGURE 6.—Proportion lactating and proportion pregnant as a function of age for sexually mature female spotted dolphins, in 1973-78 and 1981. Bars represent one standard error from the mean ($n = 542$).

of pregnant females from 1974 to 1983 (Barlow 1985) and because no significant changes were found in pregnancy rates with age, estimates of calving interval were not calculated for any of these possible stratifications.

Previous estimates of calving interval for *S. attenuata* include 2.5 yr for the southern offshore ETP stock, 2.7-3.4 yr for the northern offshore ETP stock, and 3.5-3.9 yr for a western North Pacific population (all values taken from Perrin and Reilly 1984, table 6). Our estimate, 3.06 yr, is thus close to previous estimates for the ETP northern stock and falls between the estimates for two other populations.

Lactation Period

The calving cycle in mammals can be thought of as a gestation period, a lactation period, and (in some cases) a resting period. Since gestation and lactation can overlap, the calving interval can be less than the sum of the gestation and lactation periods.

In this study, the duration of the lactation period was estimated as the fraction of mature females that are lactating multiplied by the calving interval in years. Again, the assumption is that all reproductive stages of mature females are sampled without bias. The estimated lactation period for the overall sample is 1.66 yr.

Unlike the percent pregnant, the percentage of lactating females has apparently increased over the years between 1973-74 and 1981 (Table 1). Collaborative evidence is provided by Barlow (1985). Barlow's weighted regression of the percent of lactating females regressed against year predicts values of 46% lactating for 1971 and 69% for 1983. These correspond to a change in mean lactation period from 1.4 to 2.1 yr.

There were no significant differences in proportion of lactating females in different age-classes for all aged samples combined (χ^2_3 = 2.58, $P > 0.25$) (Fig. 6).

Evidence exists for considerable individual variability in calving interval and lactation period. The sum of the estimated gestation time (0.958 yr) plus the mean lactation period (1.66 yr) is about 2.6 yr; the mean calving interval, estimated as the inverse of APR, is roughly 3 yr. We might predict from this that individuals would never be simultaneously pregnant and lactating. In fact, 16% of the sampled pregnant females were lactating. This is implicit evidence of individual variability.

Postreproductive Females

Several criteria have been used to identify postreproductive female odontocetes. Perrin et al. (1976) described postreproductive spotted dolphins and Perrin et al. (1977) described postreproductive spinner dolphins, *S. longirostris*. Both studies were based on the presence of atrophic ("regressed" or "withered") ovaries. In both cases, the incidence of postreproductive females was 1% or less of the sample. In pilot whales, *Globicephala macrorhynchus*, Marsh and Kasuya (1984) found changes in the histology of the ovary, such as a decrease in the volume of the cortex and sclerosis of the arterial walls that are age related and associated with senescence. Senescent females were characterized on the basis of follicle abundance and the incidence of follicular atresia.

Postreproductive females also occurred in our sample. Nine of the mature females collected from 1973 to 1982 had atrophic ovaries and thus are considered to have been reproductively senescent. Their mean ovary weights and maximum follicle diameters were significantly different from the means of the other mature females collected during these years (*t*-test, $P < 0.005$) (Table 3, Fig. 7). None was lactating.

Evidence of decreased fertility was found in some females without atrophic ovaries. Two groups were extracted from the aged sample: 1) those specimens that had 20 or more corpora (all but one was 20 yr old or older), and 2) those specimens that were 20 yr old or older and had only four or fewer total corpora (including atretica). Of the first group (n = 12), the mean maximum follicle diameter was larger than that of the atrophic-ovary sample (*t*-test, $P < 0.005$), but the mean weights for both ovaries combined were not significantly different (Table 4). Atretic corpora constituted 24% of the total corpora, less than the frequency of atresia found in the atrophic ovaries (39%). The two specimens in this sample with the highest proportion of corpora atretica also had ovaries with maximum follicle diameter and ovary weights within the range of the atrophic ovaries; in addition, they had no CLs (corpora lutea) or Type 1 corpora. We consider these two females to have been postreproductive. Of the second group (n = 14), the mean maximum follicle diameter and ovary weight were not different from those in the sample with more total corpora, but were markedly different from those of the atrophic ovaries (*t*-test, $P < 0.025$). None of these ovaries contained corpora atretica.

Comparison of females in the two groups provides evidence that when the complement of follicles has nearly been expended (through ovulation or atresia), fertility diminishes. Of the first group, 5 of the 12

TABLE 3.—Combined ovary weights, maximum follicle diameter, and corpora counts in "non-atrophic" (normal) ovaries with no corpus lutem (n = 3,455) and atrophic ovaries (n = 9) of sexually mature female spotted dolphins collected in 1973-82.

Variable	Non-atrophic ovaries		Atrophic ovaries	
	Mean	SE	Mean	SE
Combined ovary weight	4.9	0.05	3.0	0.30
Maximum follicle diameter	2.8	0.06	0.4	0.07
Total corpora excluding atretica	6.8	0.09	12.4	1.36
Total corpora including atretica	7.5	0.11	20.9	1.13
Corpora atretica	0.7	0.04	8.4	1.67
Percent of corpora atretic	6.4	0.30	40.0	7.6

TABLE 4.—Mean age, maximum follicle diameter, ovary weight, corpora counts, and reproductive states for female spotted dolphins. Type 1 and Type 2 corpora defined by Perrin et al. (1976).

	Age years	Maximum follicle diameter (mm)	Combined ovary weights (g)	Total corpora[1]	Corpora atretica	Percent atretic	Type 1 corpora	Type 2 corpora	Pregnant/ lactating (%)
A. Females with 20 or more corpora (n = 12)									
Mean	20.2	2.7	4.2	21.3	4.7	21.9	0.5	1.4	40
SE	1.0	0.5	0.5	0.3	0.8	3.6	0.2	0.4	
B. Females 20 yr or older with four or fewer corpora (n = 14)									
Mean	22.6	2.5	5.1	2.7	0	0	0.9	0.9	100
SE	0.5	0.3	0.6	0.3	0	0	0.2	0.2	

[1] Includes atretica.

specimens were pregnant or lactating. All 14 of the second group were pregnant or lactating. Thus, the first group shows reduced fertility when compared with the second group. Marsh and Kasuya (1984) described an age-related decline in follicle abundance in pilot whales, stating that when follicles are "depleted" the animals become senescent. The reduction in fertility indicated in our sample of spotted dolphins is not strictly age-related; it is more dependent on the number of corpora (including corpora atretica) already present in the ovaries. This has been shown to be true in western Pacific spotted dolphins (Kasuya et al. 1974) and in sperm whales (Best 1967).

In addition to the postreproductive females with atrophic ovaries, four mature females with normal-appearing ovaries had no macroscopic follicles (one of the atrophic ovaries contained no macroscopic follicles). This is similar to the condition described by Marsh and Kasuya (1984). The ovaries of these specimens weighed from 2.2 to 5.9 g, had no CLs or Type 1 or Type 2 corpora, and contained 8-22 total corpora, 12% of which were atretic. None were lactating. They are considered to have been postreproductive also.

Spotted dolphin specimens were judged to have been senescent when they had atrophic ovaries or lacked macroscopic follicles. Such specimens have in common: 1) the absence of CLs and Type 1 corpora, 2) a large number of total corpora, 3) a high frequency of atresia (a relatively large proportion of the total corpora), and 4) a maximum follicle diameter of 0.5 mm or less. The incidence of obvious senescence in the sample of spotted dolphins (0.4%) is much less than that in pilot whale samples studied (5% in *Globicephala melaena* from the northern Atlantic Ocean [Sergeant 1962] and 25% in *G. macrorhynchus* from the western Pacific [Marsh and Kasuya 1984]). This may be indicative of inherent differences in the social structure or longevity between pilot whales and spotted dolphins.

CONCLUSIONS

Several of our analyses have yielded results similar to those reported previously for spotted dolphins by others, notably Perrin et al. (1976) and Kasuya et al. (1974). We found ovulation rates to have high individual variability with a markedly higher rate of corpus formation in the earlier reproductive years that decreases after a fixed number of ovulations has occurred.

The conclusions reached by Perrin (1969b) and particularly by Kasuya et al. (1974) with regard to the close correlation between color pattern and sexual maturity in spotted dolphins are also supported by our study. Ninety-six percent of the fused, 50% of the mottled, and only 4% of the speckled specimens were sexually mature. Fused specimens had more corpora and appeared to have been sexually mature longer than mottled specimens of the same age or length.

Our estimated length of the calving interval (3.03 yr) is within the range of earlier estimates calculated for this stock by Perrin and Reilly (1984). It is also within the range of estimates for two other spotted dolphin stocks.

Some of our analyses, however, produced results

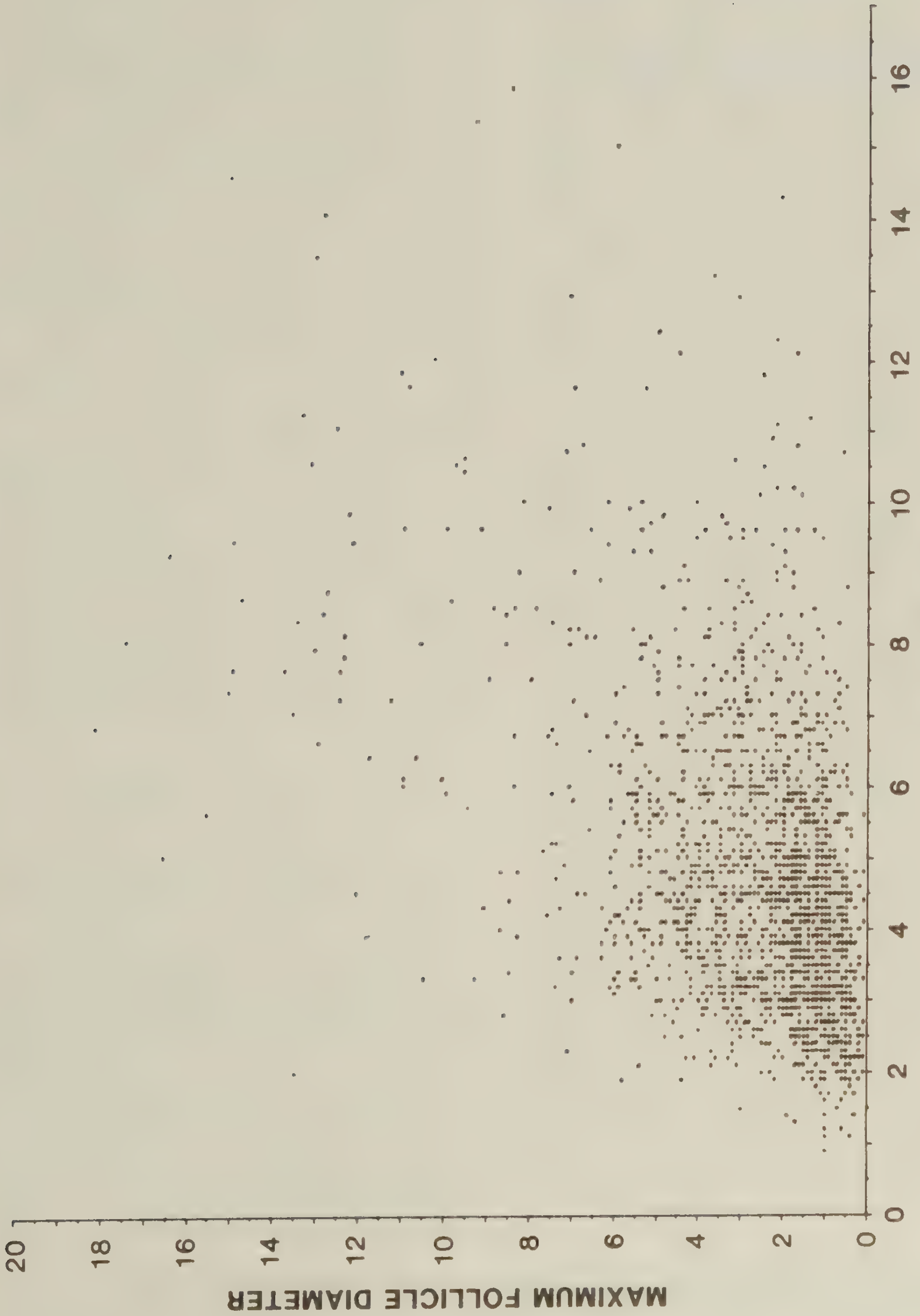

FIGURE 7.—Plot of maximum follicle diameter (mm) on combined ovary weight (g) for 3,464 female spotted dolphins.

that contradict earlier findings. Based on the more reliable method of estimating age in spotted dolphins, we believe that our findings present a clearer picture of the reproductive information than has been reported previously. Our aged samples showed that the youngest sexually mature female was 10 yr old—the same age as the youngest pregnant and the youngest lactating specimens. This suggests that some females must become sexually mature before the age of 10, even though mature specimens younger than 10 were not found in our sample. The average age of a pregnant female in our sample was about 18 yr, and some females of about 35 yr old were pregnant or nursing. These values are substantially higher than estimated previously for this stock (Perrin et al. 1976), but they are similar to, though still somewhat higher than, estimates for the western Pacific stock (Kasuya 1976).

The ASM estimate in this study (about 11.4 yr) is higher than that estimated by Perrin et al. (1976). Our calculations showed no significant difference between the ASM calculated for the 1973-74 sample (taken during years of heavy fishing mortality) and the ASM for the 1981 sample (taken after at least 5 yr of reduced fishing mortality).

An ASM of 11.4 yr means that the youngest average age of first parturition would be 12.3 yr (11 mo later). Since not all females would conceive at first ovulation, the actual average age would be greater than this. The implication of this protracted period before reproduction and a long (3.03 yr) calving interval is that spotted dolphin survival rates must be very high in order to maintain a stable population level.

There is a significant depression in the age structure of the 1973-78 and 1981 aged sample in the 6-12 yr age classes (Hohn and Myrick in prep.[2]). Similar age-structure patterns, interpreted as reflecting some sort of schooling segregation, have been encountered in studies of other delphinids (see review by Perrin and Reilly 1984). If animals at or near the age of sexual maturity have been regularly undersampled because their schools were not targets of purse seines (Hohn and Scott 1983), the ASMs calculated for the aged samples could be upwardly biased. However, there is no evidence that the depression in the age structure represents missing animals that were sexually mature.

The annual pregnancy rate averaged 0.33 from 1973 through 1981. There were no sustained upward or downward changes in age-specific pregnancy rates with increased age. A similar result was shown by Kasuya (1976) for the western stock, although his values were somewhat lower than the rates we have estimated for the northern offshore stock. Our estimates are different from those of Perrin et al. (1976) who reported high pregnancy rates among younger specimens and a decreasing rate with increased age.

The implications of an apparent progressive increase in the lactation period are enigmatic. It is probable that the increase in lactation period reflects the decrease in per capita mortality of calves due to the more efficient releasing procedures employed by the purse seine fleet from the mid-1970's onwards. Decreased mortality of nursing calves would be reflected by an apparent increase in the number of lactating females because fewer nursing periods were ended prematurely.

Our study of postreproductive specimens suggests that fertility diminishes as the complement of follicles for a female becomes expended through ovulation or atresia. Female spotted dolphins with atrophic ovaries or with no macroscopic follicles are reproductively senescent. Although the expenditure of follicles progresses with age, reduction in fertility is not strictly age related. The occurrence of reproductive senescence in spotted dolphins in this study was negligible and the number of specimens in this state probably is of limited importance to estimates of reproductive parameters.

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Apex Predation by Yellowfin Tuna (*Thunnus albacares*): Independent Estimates from Gastric Evacuation and Stomach Contents, Bioenergetics, and Cesium Concentrations

Robert J. Olson

Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92093, USA

and Christofer H. Boggs[1]

Center for Limnology, University of Wisconsin, Madison, WI 53706, USA

Olson, R. J., and C. H. Boggs. 1986. Apex predation by yellowfin tuna (*Thunnus albacares*): independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. Can. J. Fish. Aquat. Sci. 43: 1760–1775.

Three approaches for estimating predation by yellowfin tuna (*Thunnus albacares*) were compared: (1) stomach analysis adjusted for gastric evacuation; (2) food energy required as a function of swimming speed in yellowfin tracked at sea; and (3) food intake needed to maintain observed cesium concentrations. Gastric evacuation data from captive yellowfin were best fit by linear functions of time for four foods. Fish with high lipid content (mackerel, *Scomber japonicus*) were evacuated at a slower rate (proportion per hour) than smaller fish (smelt, *Hypomesus pretiosus*), squid (*Loligo opalescens*), and small fragile fish (nehu, *Stolephorus purpureus*), all of which had lower lipid contents. Tuna captured in the eastern Pacific had daily rations averaging 3.9% of body mass based on stomach contents and gastric evacuation rates, 5.2% based on bioenergetics estimates, and 6.7% based on the cesium estimate. Swimming costs accounted for one-third to one-half of the energy budget. Annual predation by the eastern Pacific yellowfin population averaged 4.3–6.4 million metric tons during 1970–72, depending on the method used for estimating ration; 34% was frigate tunas (*Auxis* spp.). High growth and turnover rates (*P/B* ratios) of tropical tunas in contrast with low conversion and trophic transfer efficiencies suggest a trophic structure that differs from more productive ecosystems.

Les auteurs comparent trois méthodes pour l'estimation de la prédation par l'albacore à nageoires jaunes (*Thunnus albacares*) : 1) l'analyse du contenu stomacal corrigé en fonction de l'évacuation gastrique; 2) l'énergie alimentaire nécessaire présentée comme une fonction de la vitesse de nage d'albacores dont les déplacements ont été relevés en mer; et 3) l'ingestion alimentaire nécessaire au maintien des concentrations de césium observées. Les données sur l'évacuation gastrique d'albacores gardés en captivité étaient le mieux représentées par des fonctions linéaires temporelles, ceci pour quatre aliments. Les poissons à forte teneur en lipides (maquereaux, *Scomber japonicus*) étaient évacués plus lentement (proportion par heure) que des poissons plus petits (éperlans, *Hypomesus pretiosus*), des calmars, *Loligo opalescens* et un petit poisson fragile (néhu, *Stolephorus purpureus*), tous à teneur en lipides moins élevée. La ration quotidienne des albacores capturés dans l'est du Pacifique s'élevait en moyenne à 3,9 % de la masse corporelle, sur la base du contenu stomacal et des taux d'évacuation gastrique, de 5,2 %, sur la base des estimations bioénergétiques, et de 6,7 %, sur la base des concentrations de césium. L'énergie consacrée à la nage représentait du tiers à la demie du bilan énergétique. La prédation annuelle de la population d'albacores de l'est du Pacifique s'est élevée en moyenne à 4,3–6,4 millions de tonnes métriques au cours de la période 1970–1972, tout dépendant de la méthode utilisée pour l'estimation de la ration; 34 % de celle-ci était composée de thazards (*Auxis* spp.). La croissance rapide et les taux de renouvellement élevés des thons tropicaux comparativement aux faibles efficacités de conversion et de transfert trophique, portent à croire à l'existence d'une structure trophique différente de celle des écosystèmes plus productifs.

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Yellowfin tuna (*Thunnus albacares*) are abundant and ubiquitous in tropical regions of the world's oceans. Tunas are opportunistic, generalist predators (Alverson 1963; Blackburn 1968; Magnuson and Heitz 1971). Metabolic rates of tunas greatly exceed those of cold-bodied fishes (Stevens and Dizon 1982) due to their obligate continuous activity (Magnuson 1978) and high "standard" metabolic rates (Brill 1979; Gooding et al. 1981). Estimates of food consumption and an understanding of energy partitioning are needed to explain the ecological strategy of this high-cost mode of living (Stevens and Neill 1978; Kitchell 1983). The large energy requirements of yellowfin, their abundance, and their broad diet make this species useful for estimating pelagic productivity at the intermediate trophic levels occupied by their prey.

Several methods for estimating daily rates of food consumption in fishes have been employed. Direct methods entail quantifying the amount of food in the stomachs of wild-caught fish and adjusting for the gastric evacuation rate determined by laboratory experiments (Elliott and Persson 1978; Jobling 1981a). Indirect methods include constructing energy and nutrient budgets (Davis and Warren 1971; Mann 1978). Both approaches have drawbacks. Direct methods are laborious and provide infrequent point estimates of in situ feeding rate. Bioenergetics modeling of food consumption can be biased by errors in parameter estimation (Bartell et al. 1986) but are useful for evaluating the effect of temperature, body size, and activity of a predator on its food resource (Kitchell 1983). Comparing estimates of food consumption from direct and indirect methods can provide valuable independent validation of laboratory-measured bioenergetics parameters (Rice and Cochran 1984).

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[1] Present address: NOAA, National Marine Fisheries Service, SWFC Honolulu Laboratory, 2570 Dole Street, Honolulu, HI 96822-2396, USA.

In our study, three independent approaches were taken to estimate the flux of energy through a tuna population. In the first, stomach analysis on thousands of field-caught yellowfin tuna was combined with laboratory determinations of gastric evacuation rates for mixed meals of different food items to estimate the daily ration of yellowfin at sea and to estimate predation rates on various prey organisms. The second approach was to employ a model derived from energy expenditures in yellowfin as a function of size and swimming speed in the laboratory (Boggs 1984). This model was applied to swimming speeds measured by acoustic telemetry of yellowfin at sea (Carey and Olson 1982) to estimate typical energy and food requirements. In the third approach, previous determinations of trophic level and cesium concentration in yellowfin and their prey (Mearns et al. 1981) and residence time of cesium in tuna tissue (Folsom et al. 1967) were used to estimate the amounts of prey consumed by yellowfin.

This diversified investigation of food consumption by yellowfin allows for comparison and corroboration of methods, and thus overcomes some of the inadequacies of each approach. The objective was to determine if food consumption by yellowfin in nature was consistent with laboratory results showing a very high energy demand. Validation of laboratory results was sought to increase the credibility of "top-down" trophic models that use bioenergetics parameters such as predation rate (Laevastu and Larkins 1981; Polovina 1984), gross conversion efficiency (Longhurst 1983), or trophic transfer efficiency (Adams et al. 1983) of major predators to describe the trophic system at lower levels. We estimated these parameters for yellowfin tuna, a dominant apex predator in the eastern tropical Pacific Ocean, and used them to estimate the minimum production rate of a variety of prey types.

Materials and Methods

Gastric Evacuation Experiments

Experimental yellowfin were caught by pole-and-line boats using live bait. They were delivered to the Kewalo Research Facility (Nakamura 1972) of the National Marine Fisheries Service in Honolulu, Hawaii, within 2−6 h and placed in 40- or 700-m^3 outdoor tanks. Ambient temperature ranged from 23.5 to 25.5°C. All experiments were conducted within 45 d of capture. Yellowfin exhibit the least degenerative physiological change of any tuna species in captivity. Individuals have been maintained for several years and have gained mass up to 50 kg (C. H. Boggs, pers. obs.).

Sixty-nine yellowfin averaging 36.2 cm in fork length (range = 23.6−45.1 cm) and 973 g (range = 220−1756 g, excluding stomach contents) were individually tagged (with color codes) for easy recognition and were trained to accept mixed meals of dead mackerel (*Scomber japonicus*), squid (*Loligo opalescens*), smelt (*Hypomesus pretiosus*), and nehu (*Stolephorus purpureus*). The foods were selected based on their taxonomic and/or gross morphological similarity to important yellowfin prey in the eastern Pacific (Alverson 1963; Anonymous 1984). Red crabs (*Pleuroncodes planipes*), an important prey, were offered but not eaten by the captive yellowfin.

All food species were acquired frozen, thawed in air, blotted, and weighed to the nearest 0.01 g. Some of the larger mackerel and squid were cut in half to allow ingestion by the yellowfin. Samples of each food type were dried at 60°C to a constant mass to determine water content. Replicate subsamples of dried specimens were analyzed for lipid content using a Soxhlet apparatus (Joslyn 1950) and chloroform−methanol, 2:1 by volume.

The yellowfin were not fed for 24 h prior to experimental feedings, allowing enough time to clear their guts. Although Noble (1973) found that fish may process food more slowly after a moderate period of food deprivation than when feeding continuously, a fairly high frequency of empty stomachs suggests that intervals without food are typical for tunas (Alverson 1963). Mixed meals of the four food organisms were offered, one food particle at a time. The time that each preweighed food particle was eaten by each individually recognized (tagged) fish was recorded to the nearest minute. Feeding continued until the tuna were satiated. The elapsed time from ingestion of each food particle to the time the fish were killed was recorded. Freshly killed fish were weighed to the nearest gram, and fork length was measured to the nearest millimetre. Hemostats were used to ligate the alimentary canal at the esophagus and pyloric sphincter. The stomach was removed from the yellowfin, slit, and the food remains removed, sorted by species, blotted, and weighed to the nearest 0.01 g. The elapsed time from handling the fish to weighing the stomach contents was about 5 min. Stomach contents were oven dried at 60°C to a constant mass at 0.01 g accuracy.

The evacuation data were analyzed separately by food species. Evacuation functions[2] were fitted using wet-mass data, since wet mass was the quantity measured during stomach analysis, and we wished to calculate daily ration on a wet-mass basis. Some data were eliminated prior to curve fitting to correct for a significant bias in this type of data (Olson and Mullen 1986). The problem becomes important when the duration of gastric evacuation experiments is long enough that at least some test individuals empty their stomachs. Empty stomachs must be omitted during data analysis because the exact time they became empty cannot be determined. Prior to the time when the fastest digestors in a sample begin to empty their stomachs, the data include the full range of intraspecific variability expected. But subsequent to that time, an ever-increasing proportion of the sample representing the faster digestors is eliminated from the distribution. Thus, as postprandial time increases, the distribution becomes constricted by the time axis. Olson and Mullen (1986) showed conclu-

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[2] Functions actually represent gastric retention, but we follow convention in calling them gastric evacuation functions.

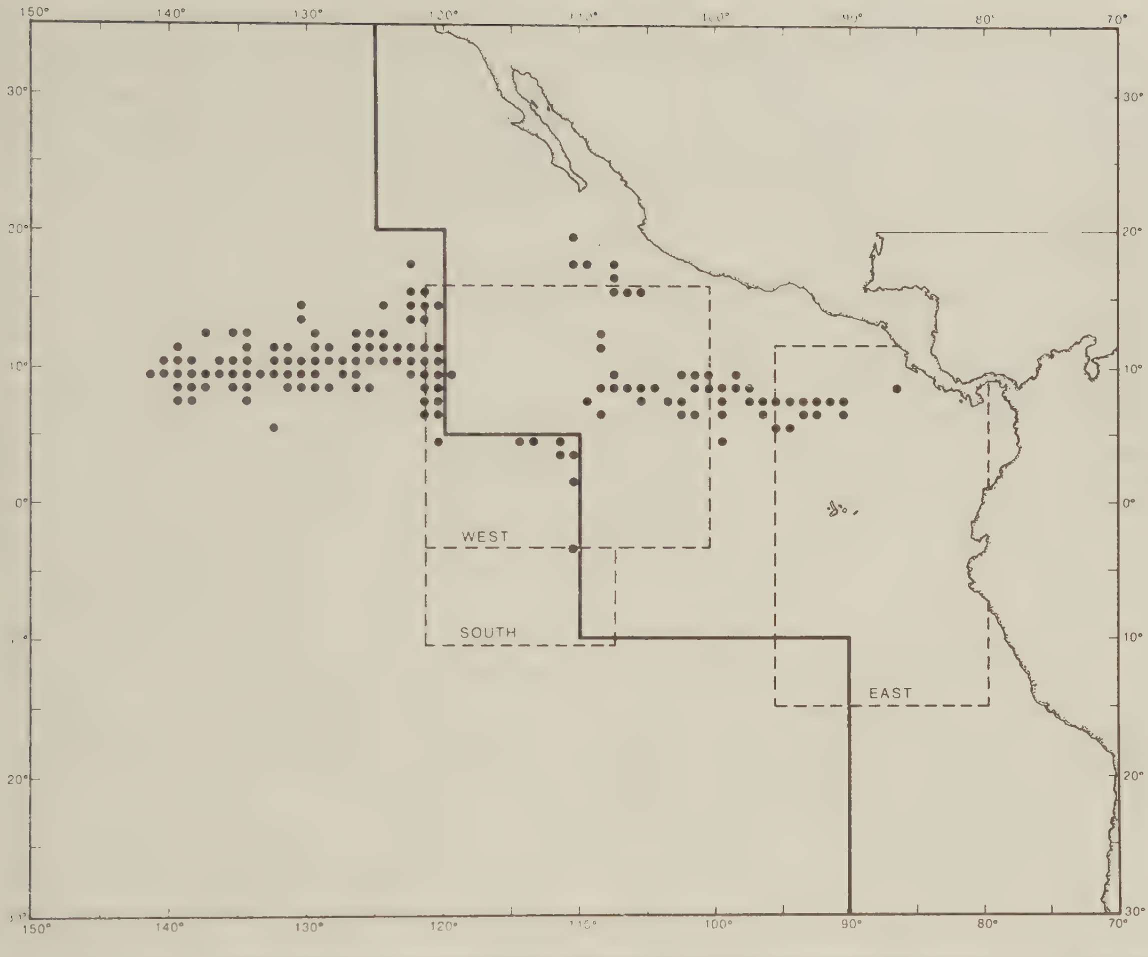

FIG. 1. Sampling locations in the eastern tropical Pacific from which stomachs of yellowfin tuna were collected during 1970–72. The western boundary of the regulated fishing area (bold line) encloses $1\,696 \times 10^{10}$ m^2 (Sharp and Francis 1976). The broken lines enclose three sampling areas of the EASTROPAC oceanographic expedition (Blackburn et al. 1970).

sively that "constricted" data distributions can cause serious bias in evacuation rate estimates and a false indication or exaggeration of curvature. Therefore, the data were truncated prior to curve fitting to eliminate those points associated with postprandial times when empty stomachs appear. A simple procedure for choosing points of truncation was explained by Olson and Mullen (1986).

The gastric evacuation data were fitted to linear, square root, and exponential models and the fits evaluated using residual mean squares and statistical procedures of residual analysis, including tests for normality (Filliben 1975), homoscedasticity, and autocorrelation (Wesolowski 1976). The Y_i values (proportion of initial amount recovered from the stomach) were transformed as $\ln(Y_i + 1.0)$ and $\sqrt{Y_i + 0.5}$ for the exponential and square root models, respectively (Zar 1974). An arcsine transformation was attempted, but did not improve the approximation of this proportion data to normality. The data were analyzed for the effect of food type, meal size, yellowfin size, mixed meals, partial food particles, and food composition on evacuation rates using analysis of covariance (Dixon and Massey 1957).

Stomach Samples

Yellowfin stomach samples from fish captured by the eastern tropical Pacific purse-seine fishery during 1970–72 (Fig. 1) were collected by scientific technicians at tuna canneries in San Diego and San Pedro, California. These yellowfin were captured during daylight hours, and most often in schools associated with dolphins (*Stenella attenuata* and *S. longirostris*). Fork length of sampled fish was measured to the nearest millimetre and the stomachs were preserved by freezing.

Stomach contents were identified to the lowest possible taxa, counted, and weighed to the nearest 0.1 g. After removing the food, the stomachs were weighed to the nearest 1.0 g. This was used to adjust for the often missing anteriormost portion of the stomachs due to the canneries' method of eviscerating tuna. A relationship between complete empty stomach mass and yellowfin fork length was determined from an independent sample of 95 yellowfin which we eviscerated. In partially filled complete stomachs the contents were distributed fairly evenly throughout the stomach. Thus, it seemed reasonable that the proportion of each prey category in the stomach contents (if any) missing from each sample was proportional to the weight of the stomach missing.

A second adjustment was made to account for reduced stomach contents due to gear retention and disturbance, since feeding presumably ceases when dolphins and associated yellowfin are chased and while enclosed in a purse seine, but digestion continues at least until death or freezing. The average duration of pursuit and enclosure was determined for fishing operations in the early 1970's and used in conjunction with evacuation rates to adjust upward the weight of stomach contents at time of gut removal.

Stomach contents data were stratified into arbitrary age-classes based on yellowfin fork length. Age-class subdivisions were selected to approximate the sizes of yellowfin upon completing their first, second, and third years based on yellowfin otolith increment counts (A. Wild, Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA, pers. comm.).

In representing the relative biomass of prey types consumed, the contribution of each prey to the daily meal was determined by accounting for differences in evacuation rate of each prey. The components of the diet were expressed as proportions of the daily meal.

Ration Estimates

Since preliminary analysis indicated that the evacuation data were poorly fitted by an exponential function, even before data were omitted as described above, an alternative to those methods for calculating daily ration which require an a priori assumption of exponential gastric evacuation (e.g. Elliott and Persson 1978) was needed. A method (Robson 1970) that is appropriate for a variety of evacuation functions was described in detail by Olson and Mullen (1986). The model predicts feeding rate ($\hat{r}$, grams per hour) by dividing the mean stomach contents per predator ($\bar{W}$, grams) by the integral (A, proportion × hours = hours) of the function that best fits experimental gastric evacuation data. A represents the average amount of time required to evacuate the average proportion of all meals present in the stomach at any instant in time. For a predator that consumes a variety of prey organisms which are evacuated at different rates:

$$(1)\quad \hat{r} = \sum_{i=0}^{I} \frac{\bar{W}_i}{A_i}$$

where subscripts i refer to each of the I prey types. Daily meal is calculated by multiplying $\hat{r}$ by 24 h, and daily ration is daily meal expressed as a percent of body mass.

Bioenergetics Model

Energy requirement calculations were based on a separate study by Boggs (1984) wherein mass and energy content of starved yellowfin were compared with controls to estimate metabolic rates following the approach described by Brett (1973). The method of estimating metabolic rates from starved fish can be used to estimate rates in the field by adjusting for mass, length, and speed and by including the increase due to SDA. Brett (1973) and Boggs (1984) did not find that starvation per se reduced metabolic rate in the highly active fishes studied. The lack of postprandial metabolic increment (SDA), reduced activity, and mass loss during starvation does reduce metabolic rate (Beamish 1964; Glass 1968; Jobling 1980a). However, nonfeeding, mass-specific, speed-specific metabolic rates are not reduced by starvation (Jobling 1980a). In Boggs's (1984) experiments the volitional speeds maintained by tuna differed between individuals, and other individuals were forced to swim fast by altering buoyancy and lift (Magnuson 1970, 1973, 1978). The effects of mass, speed, and length on the metabolic rates of 21 yellowfin were used by Boggs (1984) to fit a model for standard metabolism ($\dot{E}_0$, joules per gram per day) plus swimming work ($\dot{E}_V$, joules per gram per day) where

$$(2)\quad \dot{E}_0 = aM^{\beta}$$

$$(3)\quad \dot{E}_V = fV^{\gamma}L^{\delta}$$

where M is wet mass (grams), V is speed (centimetres per second), L is fork length (centimetres), and a, β, f, γ, and δ are empirically determined constants.

Horizontal and vertical movements of four yellowfin were tracked by Carey and Olson (1982) using acoustic telemetry. The vertical vector of the movements was ignored, since calculations indicated that horizontal movements accounted for almost 100% of distance covered. Swimming speeds were grouped in increments of 0.5 body lengths$\cdot$s^{-1}, and the average speed (centimetres per second) and total tracking duration (hours) in each increment were calculated. Then, equation 3 was used to calculate the cost of locomotion ($\dot{E}_V$) for the mean speed in each increment for the four tracked yellowfin.

The sum of locomotory costs at each speed increment was added to standard metabolism ($\dot{E}_0$). Growth rates (grams per day) for eastern Pacific yellowfin of the sizes tracked by Carey and Olson (1982) were calculated based on a size–time relationship determined from recent yellowfin otolith increment counts (A. Wild, pers. comm.) and a previous tetracycline increment validation study (Wild and Foreman 1980). Growth (grams per day) was transformed into joules per day ($\dot{E}_G$) assuming a caloric density of $6.03 \times 10^3\ \mathrm{J \cdot g^{-1}}$ for wild yellowfin (Boggs 1984). Energy losses due to excretion, egestion, and food assimilation were assumed to account for 35% of the energy consumed in food (Kitchell et al. 1978). Thus, total energy requirements (joules per gram per day) were estimated at

$$(4)\quad \frac{\dot{E}_0 + \dot{E}_V + \dot{E}_G}{1 - 0.35}.$$

Cesium Budget

The rate of cesium intake was assumed to balance the rate of cesium loss and to maintain the measured cesium concentration in yellowfin (Mearns et al. 1981) during growth. The rate of loss in yellowfin was assumed to be comparable with the biological half-life of cesium in albacore, *Thunnus alalunga* (Folsom et al. 1967; Young 1970), which is similar to that in other marine fishes (Baptist and Price 1962). A 50% decrease in concentration over 53 d (Folsom et al. 1967) is equivalent to an exponential decline ($\mathrm{Cs_{out}}$) in total cesium content of about 1.3%$\cdot$d^{-1}. Growth (G) was estimated at 0.63% wet mass$\cdot$d^{-1} (=percent cesium content per day) for the average-sized yellowfin measured by Mearns et al. (1981). A reasonable value (0.8) (Isaacs 1972) was assumed for cesium assimilation efficiency. Yellowfin cesium concentration ($\mathrm{Cs_Y}$, micrograms per kilogram wet mass) was several times greater than prey cesium concentration ($\mathrm{Cs_P}$) (Mearns et al. 1981). Thus, food intake (F, percent body mass per day) was calculated as

$$(5)\quad F = \frac{(\mathrm{Cs_{out}} + G)\,\mathrm{Cs_Y}}{(0.8)\mathrm{Cs_P}}.$$

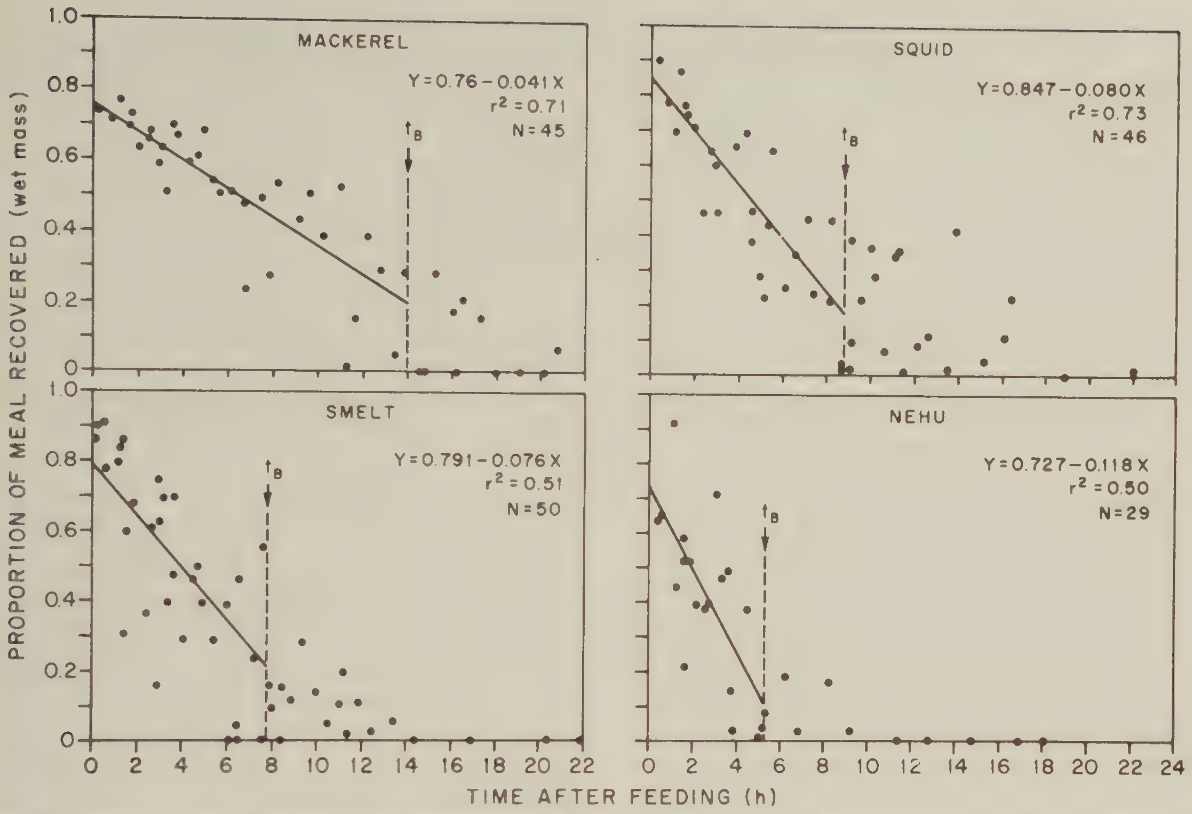

FIG. 2. Proportion of initial wet mass of four experimental foods recovered from the stomachs of captive yellowfin versus time after feeding. T_B is the point beyond which data were omitted prior to curve fitting (see text).

The total cesium concentration in the diet was determined from the values given by Mearns et al. (1981) using the proportions of different prey in the diet of age-class 1 and 2 yellowfin in this study. The cesium concentration of squid was used for cephalopods and other invertebrates and that for frigate tuna (*Auxis thazard*) was used for scombrids. The cesium concentration of flyingfish was used for all other fishes. This latter value was assumed, since these other fishes were generally smaller and thus were probably at a trophic level closer to that of flyingfish than that of frigate tuna.

Results and Discussion

Gastric Evacuation

The experimental yellowfin became satiated after about 30 min of feeding. Mean sizes of the four food organisms and the various combinations in which they were consumed are presented in Tables 1 and 2, respectively. Wet mass of the experimental meals averaged 77.1 g (N = 69, σ = 36.4 g, range = 15.8−164.8 g) and was positively correlated (r = 0.424, $P < 0.001$) with predator wet body mass (less food mass in the stomach). Relative meal size averaged 8.53% of wet body mass (σ = 3.88%, range = 1.31−18.31%) and was negatively correlated ($r = -0.438$, $P < 0.001$) with wet body mass. Subtracting mean water content per food type (Table 1) resulted in a mean experimental meal of approximately 18.9 g (σ = 8.9 g, range = 3.8−40.2 g) dry mass.

TABLE 1. Mean size, water content, and lipid content of four experimental foods used in the gastric evacuation experiments (standard deviation in parentheses).

Food species	Mean mass (g)	Mean length (mm)[a]	% water	% lipid Dry mass	% lipid Wet mass	N
Mackerel	62.9	188	73.7	30.7(2.2)	8.1(0.6)	7
Squid	53.2	160[b]	76.8	19.1(1.0)	4.4(0.2)	4
Smelt	17.8	126	76.5	23.6(1.1)	5.5(0.3)	5
Nehu	0.4	40	76.2	18.0(1.2)	4.3(0.3)	4

[a] Fork length.
[b] Length excludes tentacles.

Amounts of the four food types (proportion of initial wet mass) recovered from the yellowfin stomachs as a function of time after feeding are presented in Fig. 2. Prior to curve fitting, the data were truncated at postprandial times marked t_B (Fig. 2) to avoid a serious bias resulting from distributions constricted by the X-axis (Y = 0) (Olson and Mullen 1986). For data with variance comparable with that of Fig. 2, Olson and Mullen (1986) found, using Monte Carlo simulations, that data constriction causes the slope to be biased by about 18% ± 9% (mean ± 1 SD). This can cause the illusion of a tail (reduced slope) at later stages of digestion, which may partly explain why curvilinear functions are commonly used with this type of

TABLE 2. Mixed meal combinations of mackerel (M), squid (Sq), smelt (Sm), and nehu (N) ingested by the experimental yellowfin. Individual food particles were numbered, weighed, and fed in order to individually color-code tagged yellowfin.

Combination No.	Food species	Number that ate meal combination
—	M	2
—	Sq	2
—	Sm	2
—	N	1
1	M, Sq	10
2	M, Sm	3
3	M, N	4
4	Sq, Sm	10
5	Sq, N	1
6	Sm, N	2
7	M, Sq, Sm	11
8	Sq, Sm, N	6
9	M, Sm, N	9
10	M, Sq, Sm, N	6

data. The only option to circumvent this problem was to omit some data.

Several different mathematical models have been utilized to describe the time course of stomach emptying in fishes, including a linear model (e.g. Swenson and Smith 1973; Jones 1974), an exponential model (e.g. Elliott and Persson 1978), and a square root model (e.g. Jobling 1981a). The four data sets (Fig. 2, $X_i < t_B$) were fitted to these three models. For all four food types, residual mean squares (untransformed) of the three fits were homogeneous ($F_{\max}$-test, $P > 0.05$, Sokal and Rohlf 1969). Therefore, residual analysis was used to evaluate the fits. For all four food species, residual analyses indicated that the linear model gave a superior fit, and these regressions (Fig. 2) were accepted to represent gastric evacuation rates in yellowfin.[3] The data for dry mass recovered from the stomachs also appeared to be linear. For comparison purposes, Olson and Mullen (1986) fitted the complete unedited data sets (less empty stomachs) to the same three functions. Again, residual mean squares failed to indicate a superior fit to any of the functions ($F_{\max}$-test, $P > 0.05$, Sokal and Rohlf 1969). Residual analysis showed that the linear model gave the best fit for three of the four foods. The squid data were best described by the square root function. Although the exponential model is conceptually more satisfying than the linear model, concensus shows that linear gastric evacuation is plausible for piscivorous fishes that eat large prey (Simenstad and Cailliet 1986). Previous work substantiates this (Swenson and Smith 1973; Diana 1979; Adams et al. 1982).

It is noteworthy that the intercepts of the regression lines fall considerably below 100% (Fig. 2). Wet mass of the food in the stomachs a few minutes after feeding was considerably less than the wet mass of food prior to feeding. Magnuson (1969) found the same phenomenon when feeding smelt to skipjack tuna (*Katsuwonus pelamis*). In Magnuson's experiments, an average of 17.3% of the wet mass of smelt was lost from the food within a few minutes after ingestion. In our experiments, 20.9% of the wet mass of smelt was quickly lost. Magnuson theorized that this loss was equal to the mass of water absorbed by the food during the process of thawing in fresh water. In the present experiments, all food items were air-thawed. Nevertheless, the most plausible explanation for this sudden decrease in food mass is water loss, as there were no visible signs of digestive action on the food particles removed from fish killed within a few minutes after eating. Tuna stomachs may rapidly express water from the food, resulting in a rapid initial loss of mass (Fig. 2). Subsequently, food appears to gradually rehydrate with digestive fluids to facilitate mechanical breakdown. Significant positive correlations between percent water in food removed from stomachs and time after feeding were obtained for squid ($P < 0.001$) and nehu ($0.05 > P > 0.02$); correlations were positive but not significant for mackerel and smelt ($0.20 > P > 0.10$).

Factors Affecting Evacuation Rates

The type of prey organism ingested affects significantly the rate at which food is passed from the stomachs of fishes (Windell 1978; Fänge and Grove 1979). In yellowfin, significant differences in evacuation rate occurred among the four food types (ANCOVA, $P < 0.0005$). Mackerel were evacuated at a significantly slower rate than squid, smelt, and nehu (*t*-tests for slopes, $P < 0.01$, Zar 1974), which were evacuated at about equal rates (ANCOVA, $P > 0.25$). However, intercepts of the regression lines for squid, smelt, and nehu were significantly different ($P < 0.0005$), and thus a common regression line was not adequate to describe these three data sets.

The evidence for an effect of meal size on gastric evacuation rate of fishes is equivocal. Large meals may take longer to be totally eliminated from the stomach than small meals (Barrington 1957; Steigenberger and Larkin 1974; Jones 1974). However, the amount of food digested during a given time (grams per hour) may increase in proportion to meal size (Hunt 1960; Kitchell and Windell 1968; see review by Windell 1978). In the latter case, the percentage of the meal evacuated per unit time remains constant, and thus the time required to evacuate a meal remains approximately the same regardless of food volume (Magnuson 1969; Tyler 1970; Elliott 1972; Bagge 1977).

The yellowfin gastric evacuation data for each food type were subdivided into three groups according to relative meal size (below 8.0%, between 8.1 and 11.5%, and above 11.6% of body mass). The results of analyses of covariance performed on the subgroups indicated that relative meal size had a significant effect on the evacuation rate of mackerel ($P < 0.0005$), but not on those of squid, smelt, and nehu. Small meals of mackerel were evacuated significantly faster than medium and large meals of mackerel (*t*-tests for slopes, $P < 0.002$). Therefore, the gastric evacuation rate for mackerel in yellowfin appears to be consistent with the hypothesis of more rapid digestion of small meals, while those for squid, smelt, and nehu seem to follow the alternative hypothesis of a constant percentage per unit time.

Mackerel are larger and appear to be considerably more digestion resistant than the other three food types. The musculature of mackerel is compact, while that of smelt and nehu tends to fall apart in the stomach, providing increased surface area for digestive activity to take place. Squid also have dense musculature; however, the body cavity is more accessible and

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[3] For calculating daily ration, another equation representing the evacuation rate for mackerel in small meals was used (equation 7). See discussion of the effect of meal size and daily ration based on stomach analysis.

TABLE 3. Observed and adjusted stomach contents (% of body mass) and size characteristics of four age-classes of yellowfin tuna from which stomach samples were taken in the eastern Pacific Ocean. Adjustments for partial stomachs and gear disturbance are described in the text.

Age-class	Fork length (mm)	Body mass (g)			Observed stomach contents			Adjusted stomach contents		
		Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
1	≤550	968	3 255	2 629	0	4.98	0.31	0	5.97	0.39
2	551−865	3 310	13 140	8 603	0	3.31	0.48	0	5.55	0.62
3	866−1220	13 187	37 914	22 655	0	4.64	0.38	0	5.50	0.52
4+	>1220	38 010	95 415	53 411	0	2.99	0.39	0	5.46	0.57

the body wall is thinner than in mackerel. These results suggest that two or more models of gastric evacuation may be applicable in a single predator, depending on prey type.

Body size is recognized as one of the principal factors which can influence gastric motility in fishes (Windell 1978; Fänge and Grove 1979). However, within the size range of yellowfin in this study, analysis of covariance showed that evacuation rates were not significantly influenced by yellowfin size ($P > 0.05$).

Whether foods that are evacuated at distinctly different rates retain their distinct evacuation rates when fed in mixed meals is unknown. Windell (1967) and Elliott (1972) reported that mixed meals of organisms that have similar evacuation rates in bluegill sunfish (*Lepomis macrochirus*) and brown trout (*Salmo trutta*) were evacuated at the same rate as the organisms separately. In the present study, no indication was found to suspect that measuring evacuation rates of food organisms in mixed meals influenced the rate determinations for each food type. For example, evacuation rates (slopes) for mackerel by yellowfin which ate meal combinations 1, 2, 3, 7, 9, and 10 (Table 2) were not significantly different (ANCOVA, $P > 0.05$).

To analyze the effect of cutting some food items into pieces, analysis of covariance was conducted on the data for each food type grouped by whole food specimens, anterior halves, posterior halves, and mixed anterior and posterior halves. Low F-ratios resulted ($P > 0.25$), indicating that the practice of cutting food items did not significantly affect the evacuation rates in these experiments.

Previous workers using prepared foods have demonstrated that low-energy foods are emptied from the stomach more rapidly than foods of high caloric content (Grove et al. 1978; Flowerdew and Grove 1979; Jobling 1981b). Elevated energy levels in natural organisms are commonly related to increased quantities of lipids in the tissues, and the presence of lipids, particularly when in excess of 15% of dry mass (Windell 1978), appears to have a retarding effect on gastric evacuation (Quigley and Meschan 1941; Windell 1967; Fänge and Grove 1979). This is generally attributed to a feedback mechanism, possibly triggered by a hormone similar to enterogastrone in mammals (Hunt and Knox 1968) produced in response to the presence of lipids or the digestive products of lipids in the duodenum (Windell 1967; Hunt 1975; Jobling 1980b).

In yellowfin, gastric evacuation rates (regression coefficients, Fig. 2) were correlated with total lipid content (Table 1) (lipid as percent wet mass: $r = 0.885$, $N = 20$, $P < 0.001$; lipid as percent dry mass: $r = 0.888$, $N = 20$, $P < 0.001$) and calories per gram of wet mass ($r = 0.983$, $N = 20$, $P < 0.001$) of the food. It appears, then, that the relationships between caloric content, total lipid content, and evacuation rate found for prepared foods hold true for the natural food organisms tested here. Thus, the high lipid content of mackerel could explain its slow evacuation rate in yellowfin.

Rapid Evacuation Rates in Tunas

This study provides evidence that yellowfin evacuate food from the stomach faster than most other fishes studied, and at about the same rate as skipjack tuna. Magnuson (1969) found that only 1 of 12 species of carnivorous fishes he reviewed had a higher rate of emptying than skipjack. Yellowfin and skipjack emptied their stomachs of smelt in an average of 10.4 and 12 h (Magnuson 1969), respectively. Other piscivores of similar body length reviewed by Magnuson required four to five times longer than skipjack to evacuate a meal. Experiments by Steigenberger and Larkin (1974) on northern squawfish (*Ptychocheilus oregonensis*) were conducted on fish similar in size to our yellowfin, at the same water temperature, and using fish as experimental food. The squawfish required almost 2 h more to empty their stomachs of 3- to 6-cm juvenile rainbow trout (*Salmo gairdneri*) than it took the yellowfin to evacuate nehu, a comparably sized food.

Tunas are a highly specialized group of fishes that must swim continuously to maintain hydrostatic equilibrium and to ventilate their gills (Magnuson 1973; Roberts 1978). Energy expenditures for both "standard" metabolism (Brill 1979) and the metabolic work required for swimming (Gooding et al. 1981; Graham and Laurs 1982; Boggs 1984) are substantially higher than those typical of most other fishes (e.g. Brett 1972). Yet, yellowfin and skipjack are abundant in tropical seas where primary production is purported to be low (but see Kerr 1983) and the food distributions are known to be patchy (Blackburn 1968). It is advantageous for the tropical tunas to have the ability to process large amounts of food in a short time when food is available. The more rapidly food is digested and evacuated from the stomach, the more food a tuna can acquire from what may be very short-lived aggregations of prey. Any excess energy that is left after meeting metabolic demands is used for growth or stored as body lipids for reproduction and migration (Sharp and Dotson 1977).

Consumption Estimates

Stomach contents and gastric evacuation

Total adjustments of prey mass for partial stomachs and gear disturbance by age-class in the 1970−72 stomach samples amounted to increases of 26−46% of the mean observed stomach contents (Table 3). A relationship between complete empty stomach mass (Y, grams) and yellowfin fork length (X, millimetres) was used to adjust for partial stomachs:

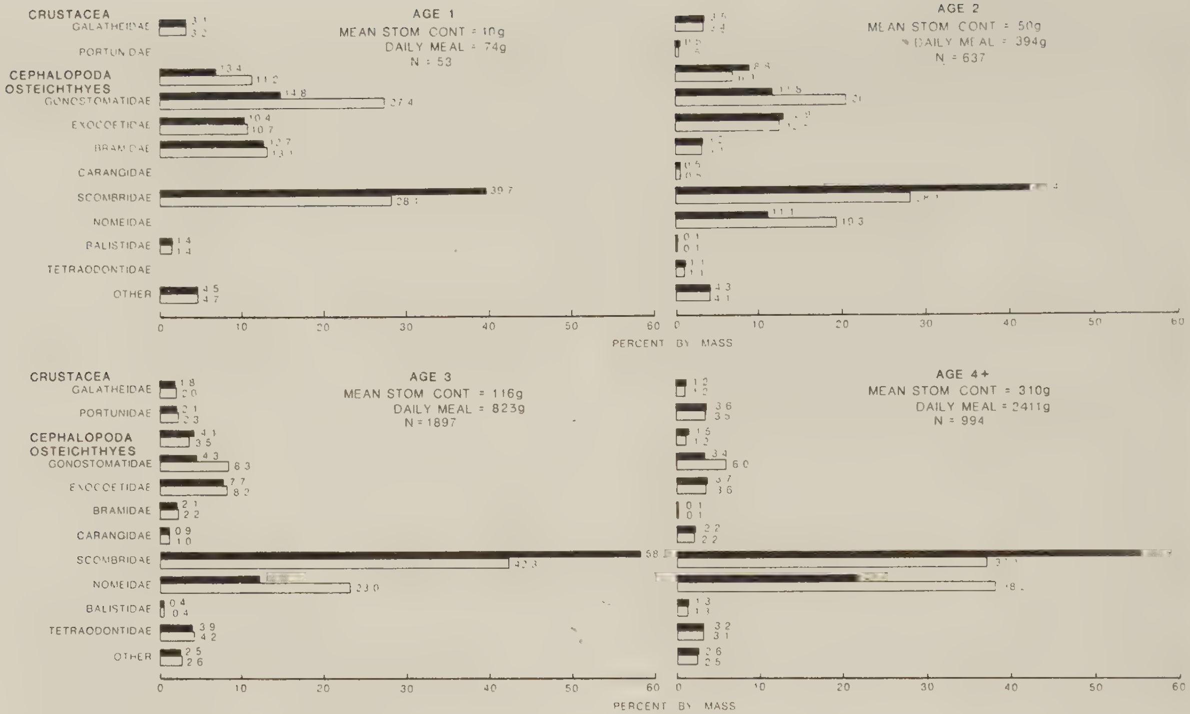

FIG. 3. Percent by mass of adjusted stomach contents (black bars) and of daily meal (white bars) for prey found in yellowfin stomachs sampled during 1970–72.

(6) $\ln Y = -12.61 + 2.59 \ln X$ ($r^2 = 0.968$).

The average duration of pursuit and gear enclosure by purse seiners in the early 1970's (2.25 h) and the gastric evacuation functions (Fig. 2) were used to calculate adjustments for reduced stomach contents due to fishing gear disturbance. The effect of this adjustment was to increase ration by about 25%.

Mean adjusted stomach contents pooled ranged between 0.39 and 0.62% and maximum adjusted amounts between 5.46 and 5.97% of wet body mass (Table 3). Yellowfin prey were matched with the most similar food organisms tested in the gastric evacuation experiments (Table 4). We assume that the evacuation functions for mackerel, squid, and nehu in small captive yellowfin approximate those of frigate tunas, cephalopods, and gonostomatids/nomeids, respectively, in wild yellowfin. The mean gastric evacuation rate and intercept for the four experimental food organisms (Table 4) were assumed to approximate those of all other prey in yellowfin stomachs. The error created by application of the mean rate to organisms with chitinous exoskeletons is probably not too important to the total ration estimate because crustaceans represented only 3.1–4.8% by mass of the stomach contents (Fig. 3). Since the stomach contents indicated that small meals are common, and meal size had an effect on the evacuation rate of mackerel, the regression equation (from ANCOVA above) for mackerel in small meals was used to calculate A_i for the Scombridae:

(7) $Y = 0.856 - 0.0693X$ ($r^2 = 0.925$).

Estimates of average hourly feeding rate, $\hat{r}$, for eastern Pacific yellowfin were calculated from equation 1 using values for $\overline{W}_i$ and of A_i from data in Fig. 3 and Table 4, respectively. Empty stomachs were included for calculating $\overline{W}_i$, since they, as well as full stomachs, reflect the natural feeding condition of the population. Yellowfin are known to feed in the daytime as well as at night (Watanabe 1958; Kume and Morita 1966). Lacking quantitative evidence for diel differences in feeding rate, we have assumed a daily feeding period of 24 h (steady state), recognizing that under some circumstances, nighttime feeding may decline or not occur, which would reduce ration estimates by as much as 50%. Daily meal, then, is assumed to be $24\hat{r}$. Daily rations are the daily meals expressed as a percent of mean mass of yellowfin sampled in each age-class (Table 3).

TABLE 4. Yellowfin prey categories, corresponding gastric evacuation rates (b_1) and intercepts (b_0) from linear regressions fit to evacuation data for mackerel in small meals[a] (M), squid (Sq), and nehu (N) (Fig. 2), mean b_1 and b_0 of M, Sq, N, and smelt (Sm) regressions, and A's used in the food consumption model (equation 1). A's were calculated as the area (integral) under the evacuation function: $A = |b_0^2/2b_1|$ (hours).

Prey	Experimental food species	Regression values		A
		b_1	b_0	
Scombridae	M	−0.0693[a]	0.856[a]	5.29
Gonostomatidae	N	−0.1182	0.727	2.24
Nomeidae	N	−0.1182	0.727	2.24
Cephalopoda	Sq	−0.0800	0.847	4.48
Others	Mean of M, Sq, Sm, N	−0.0859	0.805	3.77

[a] From equation 7.

The initial reduction of wet mass immediately following ingestion in yellowfin is not accounted for in calculating $\hat{r}$ from equation 1. This phenomenon probably occurs with prey in nature as well as in the laboratory. Thus, in calculating daily rations for yellowfin in the eastern Pacific, $\hat{r}$ values were increased by the difference between 100% and the intercept for each food type (Table 4).

Mean daily rations were 2.8, 4.6, 3.6, and 4.5% of body mass per day for age-classes 1, 2, 3, and 4+, respectively. The expected decrease in daily ration with increased size (Kitchell et al. 1978) was not observed. Perhaps the ration of the smallest age-class was poorly represented through some selectivity in the catch. Although the estimated rations are similar to daily rations calculated for small fishes using field data (Seaburg and Moyle 1964; MacKinnon 1973a, 1973b; Swenson and Smith 1973; Lane 1975; Thorpe 1977; Diana 1979; Lane et al. 1979), they are larger than expected for fish of this size.

The tendency to overestimate ration by the assumption of a 24-h feeding period may be offset due to negatively biased stomach samples. Sampling difficulties and an unknown rate of regurgitation during capture would reduce the apparent food mass in stomach samples. Also, gastric motility presumably ceases at death, but digestion is a chemical process that may continue at a reduced rate until the stomach is frozen (Eggers 1977) and after thawing.

Average daily food consumption by eastern Pacific yellowfin appears to be a small fraction of the maximum possible rate, as evidenced in the laboratory and in the field. Assuming that fish with full stomachs could have continued feeding on the same prey at a rate sufficient to maintain that quantity in the stomachs for 24 h, maximum daily rations would average about 40% of body mass. This is higher, but not double, the maximum rations determined for 1.4-kg skipjack fed small food particles ad libitum for a 12-h daylight period (28−35% of body mass) (Kitchell et al. 1978).

Estimates from bioenergetics

The mass-specific rate of "standard" metabolism in skipjack tuna was found to decrease significantly with increasing mass in spinalectomized skipjack by Brill (1979). This decrease ($\beta = -0.44$, equation 2) was greater than in other fishes. By extrapolating from swimming metabolism to zero speed, Gooding et al. (1981) found that standard metabolism increased significantly with mass ($\beta = 0.19$). No significant effect of mass on standard metabolism (determined by extrapolation) was found by Boggs (1984). These contradictory results may be related to a small range in mass in the latter two studies. The mean value for standard metabolism ($\dot{E}_0$) determined by Boggs (1984) for yellowfin was 38.4 $J \cdot g^{-1} \cdot d^{-1}$ ($a = 38.4$, $\beta = 0$, equation 2).

Boggs (1984) found that mass-specific swimming metabolism ($\dot{E}_V$) of yellowfin had a length exponent (δ) of −1.28, a speed exponent (γ) of 1.64, and a coefficient (f) of 13.7. The speed exponent (γ) was lower than the 2.5−2.8 predicted by hydrodynamic theory (Wu and Yates 1978) but similar to the exponent (1.9) resulting from reanalysis of data on salmon (Wu and Yates 1978; Boggs 1984). In general, the effect of speed on metabolic rate in fishes (Beamish 1978) is less than that predicted by hydrodynamic theory.

Daily swimming costs (Table 5) calculated using equation 3 accounted for one-third to one-half of the energy budget (Table 6) of the four yellowfin tracked by Carey and Olson (1982). The mean swimming cost (weighted by the duration of each track) amounted to 100 $J \cdot g^{-1} \cdot d^{-1}$. The most frequently recorded speeds of the four tracked yellowfin were less than 100 $cm \cdot s^{-1}$ (less than one body length per second for these fish, Table 5), but faster speeds were common, and speeds as high as 300−400 $cm \cdot s^{-1}$ were maintained for over half an hour. These short times spent at high speeds contributed substantially to the total estimated cost of swimming (Table 5). Daily swimming costs varied by a factor of 4 among the four tracked yellowfin. There was a trend for speeds and locomotory costs to be low in the two fish that were tracked for a full day or longer (Table 5).

Estimates of total energy consumption ranged from 175 to 441 $J \cdot g^{-1} \cdot d^{-1}$ (Table 6). When total energy requirements were converted into a daily ration using a caloric equivalent of 4.60 $kJ \cdot g$ wet $mass^{-1}$ for food (Kitchell et al. 1978), the mean ration for 87- to 98-cm yellowfin was equivalent to about 5.2% of wet body mass per day. This was about 1.1−1.4 times the estimates from stomach contents and gastric evacuation rates for similarly sized yellowfin (age-classes 2 and 3). This suggests that the energy requirements we estimated were reasonable and that extrapolation of the empirical model for swimming costs (equation 3) did not result in values that were unrealistically low.

Sharp and Francis (1976) estimated a mean energy requirement of 319 $J \cdot g^{-1} \cdot d^{-1}$ for 12.6-kg yellowfin based on a hydrodynamic model for power output and assuming that yellowfin swim at 300 $cm \cdot s^{-1}$ for 1.2 h per day and at near minimum speeds (Magnuson 1973) the rest of the day. Sharp (1984) used the same hydrodynamic model to estimate an average energy requirement of 232 $J \cdot g^{-1} \cdot d^{-1}$ for two yellowfin tracked by Carey and Olson (1982). Both of these estimates (Sharp and Francis 1976; Sharp 1984) are within the range of total energy expended estimated using equation 4 (Table 6). Sharp and Francis's (1976) model includes the effects of transition between laminar and turbulent boundary layer conditions. If the velocity exponent does increase radically at Reynold's numbers above about 10^6 (Sharp and Francis 1976), then the values given in Tables 5 and 6 could be underestimates.

Energy can be supplied from stored reserves of fat as well as from food consumption. Thus, bioenergetics estimates of required energy may exceed actual consumption over a short term. Of course, fat reserves are ultimately derived from surplus energy intake, but the feeding conditions that permit such fat storage are probably not represented by the average stomach contents observed in the field. It is clear from our laboratory studies that yellowfin can eat much more than the overall average rates indicate, and it is clear from field studies that fat content in tunas is highly variable and can increase dramatically in certain areas (Dotson 1978; Vlieg et al. 1983). Tuna bioenergetics may be pictured as "speculative" (Stevens and Neill 1978) in the sense that tuna may exhaust their energy reserves in migrating hundreds of kilometres (Sharp and Dotson 1977) to reach good foraging habitats. This gamble must succeed frequently enough to permit rapid rates of growth among survivors, but the gamble must sometimes fail, resulting in energy depletion, disease, and vulnerability to predation. This would help explain the high natural mortality rates of tuna (Murphy and Sakagawa 1977). Depletion of fat reserves during reproduction would increase the potential for severe energy depletion and might explain reports that sex ratios are skewed strongly towards males in very large yellowfin (Cole 1980; Anonymous 1983). Further investigation of fat dynamics could suggest patterns in foraging behavior,

TABLE 5. Speeds and swimming costs of four yellowfin tuna tracked by Carey and Olson (1982). Observed speeds were grouped by 0.5 body lengths (bl)·s^{-1} increments. The average speed and the total time spent in each increment were used to calculate swimming costs.

Fish ID No. (fork length)	Speed interval (bl·s^{-1})	Mean speed (cm·s^{-1})	Power output (J·g^{-1}·h^{-1})	Duration (h)	Swimming cost (J·g^{-1})	Daily swimming cost (J·g^{-1}·d^{-1})
2	0–0.5	40	0.8	0.4	0.3	
(87 cm)	0.5–1.0	77	2.4	2.1	5.1	
	1.0–1.5	118	4.9	2.0	9.7	
	1.5–2.0	152	7.4	1.5	11.4	
	2.0–2.5	189	10.6	1.4	14.5	
	2.5–3.0	236	15.3	0.7	11.4	
	3.0–3.5			0	0	
	3.5–4.0	274	19.6	0.3	5.9	
	4.0–4.5	377	33.1	0.4	14.3	
	4.5–5.0	396	36.8	0.4	15.5	
			Total	9.3	88.2	228
3	0–0.5	38	0.7	4.9	3.9	
(89 cm)	0.5–1.0	67	1.9	19.4	36.1	
	1.0–1.5	115	4.6	11.1	50.6	
	1.5–2.0	150	7.1	9.8	69.6	
	2.0–2.5	186	10.1	0.7	7.0	
	2.5–3.5			0	0	
	3.5–4.0	316	24.0	0.2	4.0	
			Total	46.1	170.9	89
4	0–0.5	34	0.6	2.1	1.1	
(98 cm)	0.5–1.0	70	1.8	5.9	10.5	
	1.0–1.5	120	4.3	4.9	21.1	
	1.5–2.0			0	0	
	2.0–2.5	219	11.6	1.4	16.8	
	2.5–3.0	294	18.8	0.5	10.0	
	3.0–3.5	295	19.0	0.2	3.5	
	3.5–4.0	370	27.5	0.5	14.2	
			Total	15.5	77.3	120
5	0–0.5	31	0.5	11.2	5.4	
(96 cm)	0.5–1.0	66	1.6	7.2	11.8	
	1.0–1.5	117	4.3	3.6	15.4	
	1.5–2.0	177	8.4	0.7	6.2	
	2.0–2.5	214	11.5	0.3	3.5	
	2.5–3.5			0	0	
	3.5–4.0	354	26.3	0.6	14.5	
			Total	23.6	56.7	58
			Grand total	94.5	393	

energy utilization, and movements of tunas.

An estimate from cesium concentrations

The proportions of food in the diet (stomach contents adjusted for differential rates of gastric evacuation) of age-class 1 and 2 yellowfin (white bars, Fig. 3) were used to represent those of a typical yellowfin in the size range used by Mearns et al. (1981) in their measurements of cesium concentrations. Thus, approximately 28% of the diet (by wet mass) was frigate tunas and other scombrids, 12% was squid and other invertebrates, 12% was flyingfish, and 48% was other fishes (34% gonostomatids and nomeids). Assigning these proportions (Materials and Methods) to the cesium concentrations of prey given by Mearns et al. (1981) resulted in an estimate of total dietary cesium concentration (Cs_P) of about 21.8 μg·wet kg food^{-1}. Yellowfin cesium concentration (Cs_Y) was given as 60.5 μg·wet kg^{-1}. Thus, from equation 5 the estimated daily ration is 6.7% of body mass per day. This is 2.4 and 1.5 times higher than the estimates from gastric evacuation rates and stomach contents for yellowfin of similar size (age-classes 1 and 2, respectively). The greatest difference is due to the anomalous low ration estimate from stomach contents of age-class 1. The cesium budget estimate is 29% higher than the ration estimate from energy requirements (mean ration, Table 6). The cesium estimate was made for smaller fish than the bioenergetics model estimate, and a larger ration is expected in smaller yellowfin (Kitchell et al. 1978).

The data on cesium concentrations were limited, and the assumptions required to translate these into a ration are crude. This approach may be the least accurate of the three. However, the consistency of results from the cesium approach and the bioenergetics approach implies that stomach analysis under-

TABLE 6. Daily ration estimates (% body mass $\cdot$ d^{-1}) for four yellowfin tuna tracked by Carey and Olson (1982) based on energy expenditures for swimming, standard metabolism, growth, excretion, egestion, and food assimilation.

Fish ID No.	Fork length (cm)	Mass (kg)	Energy expended ($J \cdot g^{-1} \cdot d^{-1}$) Swimming cost (Table 5)	Standard metabolism ($\dot{E}_0$)	Growth ($\dot{E}_G$)	Excretion, egestion, and assimilation	Total consumed	Ration ($\% \cdot d^{-1}$)
2	87	13.4	228	38	21	155	441	9.6
3	89	14.3	89	38	20	79	226	4.9
4	98	19.3	120	38	18	95	270	5.9
5	96	18.1	58	38	18	62	175	3.8
Mean			100[a]	38	19		241[b]	5.2[c]

[a] Weighted mean from grand total in Table 5.

[b] From equation 4 using weighted mean swimming costs of 100 $J \cdot g^{-1} \cdot d^{-1}$.

[c] Based on total of 241 $J \cdot g^{-1} \cdot d^{-1}$.

estimates the true amount of food in stomachs of yellowfin at sea, especially in smaller fish. For comparable age-classes, the bioenergetics estimate (5.2%) averaged 1.3 times higher (ages 2 and 3) and the cesium estimate (6.7%) averaged 1.8 times higher (ages 1 and 2) than the direct estimates from stomach contents and gastric evacuation rates. Together, the indirect estimates averaged 1.5 times the results from the direct method.

Apex Predation and Trophic Relations

It is difficult to estimate biomass or production at intermediate trophic levels in pelagic marine ecosystems by direct sampling. As an alternative, bioenergetics models combined with estimates of apex predator biomass from fisheries statistics, tag and recapture studies, or surveys can be used to estimate the rate of prey production required to balance consumption by predators (Laevastu and Larkins 1981; Polovina 1984). This trophic approach can be extended down through the food web to estimate production and biomass at lower levels. The trophic model inputs are predation rates determined from studies like this one, and turnover rates determined from studies of age structure (Allen 1971) and natural mortality (Pauly 1980) or from other estimates of annual production to annual mean biomass (P/B) ratio (Banse and Mosher 1980; Adams et al. 1983; Longhurst 1983; Polovina 1984).

Total predation by yellowfin in the eastern tropical Pacific depends on the number of yellowfin in that region. Cohort analysis has been used to estimate the size of the exploited yellowfin population (Anonymous 1983) in the regulated area shown in Fig. 1. The average of estimates for 1970–72 is 4×10^7 individuals (3×10^8 kg). This population was subdivided among the four age-classes used to stratify the stomach contents data (Table 3) according to average size composition of the catch (Anonymous 1983, p. 87). Dividing the numbers and biomass of yellowfin in each age-class by the area of the regulated fishery (Sharp and Francis 1976) (Fig. 1) results in estimates of yellowfin density (Fig. 4).

Predation rates on each prey type can be estimated from their proportion in the diet. Proportions of prey in the stomach contents (black bars, Fig. 3) do not adequately represent relative biomass of prey types consumed due to differential rates of digestion and gastric evacuation (Hess and Rainwater 1939; Macdonald et al. 1982). Although Persson (1984) recommended otherwise, stomach contents were adjusted for differential rates of gastric evacuation (white bars, Fig. 3). This adjustment substantially reduced the proportion of Scombridae in the diet compared with the proportion found in stomach samples. Nevertheless, in the offshore areas (Fig. 1), scombrids (almost entirely frigate tunas, *Auxis* spp.) were the most important prey by mass in all age-classes except 4+. Small epipelagic and mesopelagic fishes, Nomeidae (mostly *Cubiceps pauciradiatus*), and Gonostomatidae (mostly *Vinciguerria lucetia*), respectively, were either first, second, or third most important prey by mass in the diet of each age-class. Exocoetidae (flyingfish) and cephalopods (mostly squids) were also important by mass. The food habits of yellowfin inhabiting inshore and island areas differ from this pattern (King and Ikehara 1956; Alverson 1963).

Total annual predation by the yellowfin population was divided into predation on each major prey type using the adjusted proportions in the diet (Fig. 4). Assuming that a long-term equilibrium exists, the energy passed from prey trophic levels to the predators represents production rather than a decline in standing stock of prey. Under this assumption, predation rates of yellowfin tuna represent minimum rates of production, and in many cases, the only estimates of production for these pelagic animals. Actual predation rates may be about 1–1.5 times higher than these estimates, since the consumption estimates based on energy requirements and cesium concentrations were about 1.5 times the consumption estimates based on stomach contents. This range (1–1.5 times) is incorporated in the following estimates.

The annual production of frigate tunas in the regulated fishing area (Fig. 1) during 1970–72 must have amounted to at least 1.4–2.1 million metric tons (t). This amount was calculated by multiplying the predation rate on Scombridae (Fig. 4) by the area of the regulated fishing region (Fig. 1) and the range in the ration estimates (1–1.5 times). This production is more than the average annual world catch of all tunas during those years (1.2 million t, FAO 1974). It amounts to about 11–17 times the average biomass of yellowfin caught in this area annually during those years (Anonymous 1983). Frigate tunas are important prey of other apex predators that inhabit the region (Uchida 1981), so these figures underestimate total production of frigate tunas. Possible interaction between frigate tunas and young stages of other tunas could have important implications on the tuna stocks. If frigate tunas prey on larval or postlarval yellowfin, then increasing the commercial harvest of yellowfin, resulting in larger standing stocks

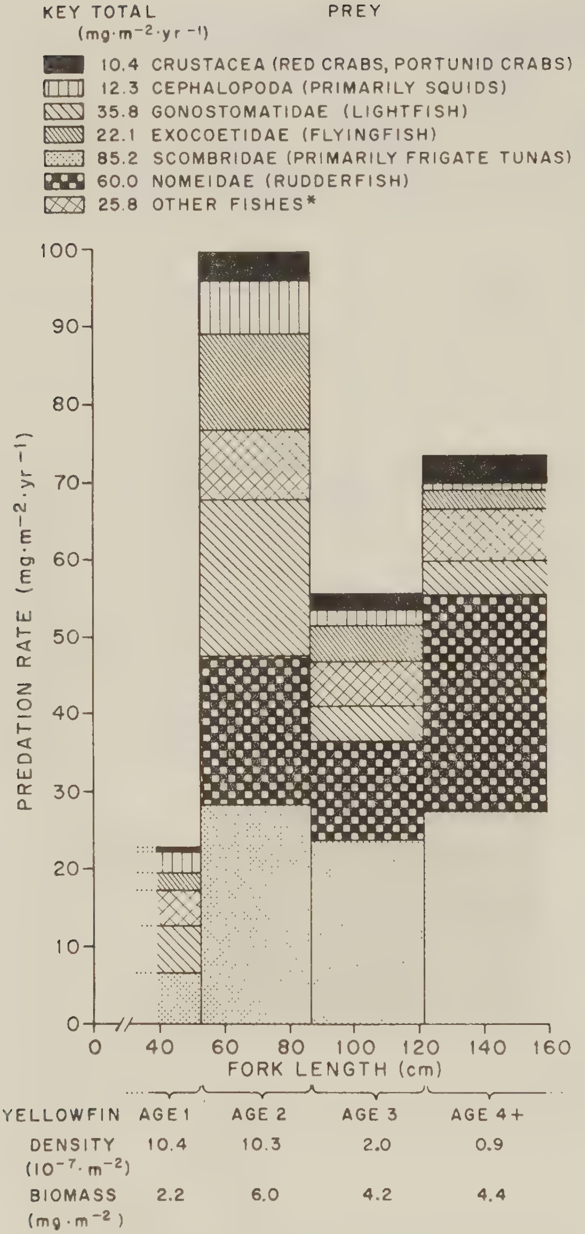

FIG. 4. Total prey biomass (mg·m^{-2}) consumed per year by the yellowfin population in the eastern tropical Pacific Ocean in 1970–72 based on stomach contents and gastric evacuation rates. Yellowfin density and biomass are given at the bottom for each age-class. *The "other fishes" category was composed primarily of Bramidae, Carangidae, Balistidae, and Tetraodontidae.

of yellowfin prey, might have a deleterious effect on yellowfin recruitment. Previous to this study there were no estimates of standing stock or production for the frigate tunas. These species are largely unexploited in the eastern tropical Pacific.

Turnover rates for frigate tunas can be approximated using an equation relating the P/B ratio to body mass (Banse and Mosher 1980) and from the natural mortality rate ($P/B = M$, Allen 1971). Average mass at maturity (400 g) and von Bertalanffy growth parameters ($L_\infty = 53$ cm, $K = 0.4$) were estimated from the sparse data summarized by Uchida (1981). The body mass relationship implies an annual P/B ratio of 0.5, but Banse and Mosher's (1980) equation was derived from data on small, temperate fishes. Empirical relationships between P/B ratios and body mass should be interpreted cautiously (McLaren and Corkett 1984). Longhurst (1983) discussed the reasons for larger P/B ratios for marine fishes in the tropics. Pauly's (1980) formula for natural mortality (M) as a function of L_∞, K, and mean environmental temperature (25°C) suggests a P/B ratio of 0.8 for frigate tunas. Fishing mortality (F) in the eastern tropical Pacific is negligable (Anonymous 1983). Based on our production estimate, this would indicate a standing stock of at least 1.7–2.6 million t of frigate tunas in the regulated fishing area (Fig. 1).

The turnover rate for the yellowfin tuna population can be approximated as the total mortality rate ($P/B = Z = M + F$). Fishing mortality averaged 0.44 during 1970–72, and natural mortality was estimated at 0.8 (Anonymous 1983). Thus, P/B was about $1.2 \cdot yr^{-1}$. In contrast, Banse and Mosher's (1980) equation gives an estimate of only 0.2 for an average mass at maturity of 30 kg (Cole 1980). Some estimates for tropical marine fishes range as high as 3.4–4.5 (Longhurst 1983). The P/B for skipjack tuna in the Pacific Ocean is about 5.3 at MSY (R. F. Francis, National Marine Fisheries Service, Northwest and Alaska Fisheries Center, 2725 Montlake Blvd East, Seattle, WA 98112, pers. comm.).

High P/B ratios could result from an abundant food supply, a high trophic transfer efficiency, or both. Using our estimate of food consumption by yellowfin tuna, we can proceed to make a direct estimate of gross conversion efficiency and trophic transfer efficiency. The average food consumption for an individual yellowfin tuna estimated from bioenergetics was 241 $J \cdot g^{-1} \cdot d^{-1}$ whereas growth was estimated at only 19 $J \cdot g^{-1} \cdot d^{-1}$ (Table 6), indicating a gross conversion efficiency of only 8%. Annual yellowfin production was about 1.2 times the standing stock of yellowfin whereas annual consumption by yellowfin was estimated at 15–22 times the standing stock of yellowfin (Fig. 4), indicating a trophic transfer efficiency of only 8–5%. These efficiencies seem low compared with those in more productive ecosystems (Kozlovsky 1968; Adams et al. 1983; Longhurst 1983; Polovina 1984).

The availability of food is difficult to address without a more complete trophic analysis. Primary production and standing stocks of phytoplankton, zooplankton, crustacean micronekton, and fish–cephalopod micronekton in the eastern tropical Pacific were measured by the EASTROPAC oceanographic expedition (Owen and Zeitzschel 1970; Blackburn et al. 1970). These studies examined areal and seasonal variations over a year (1967–68) in a comprehensive survey of a magnitude that is unlikely to be repeated. They found that the average standing stock of fish–cephalopod micronekton in the western region (Fig. 1) was about 3 $mL \cdot m^{-2}$ or about 3 $g \cdot m^{-2}$ for a 200-m water column (Blackburn et al. 1970). This is only twice as much as would be consumed annually by the estimated standing stock of frigate tunas if they ate 4% of their body mass per day.

Only 2.8% or 0.08 $g \cdot m^{-2}$ of the fish–cephalopod standing stock measured by Blackburn et al. (1970) consisted of epipelagic fishes whereas 90% (0.23–0.35 $g \cdot m^{-2} \cdot yr^{-1}$) of predation by yellowfin in the offshore regions (Fig. 1) was on epipelagic fishes, predominantly frigate tunas, nomeids, and exocoetids (Fig. 4). These estimates are not strictly comparable, since some of the prey consumed by yellowfin were larger than micronekton (1–10 cm), but they suggest some degree of scarcity and/or a high annual turnover rate for the epipelagic forage fishes.

Sharp and Francis (1976) estimated that daily consumption by the yellowfin population was small compared with the standing stocks measured by Blackburn et al. (1970). They considered the relative effective productivity at different size-related trophic levels as well as the underestimation of the standing stocks of the more mobile tuna forage species, and argued that yellowfin with fork length greater than 40 cm were not food limited. Of course, the forage available to yellowfin should be based on the productivity of their forage rather than standing stock, but Sharp and Francis were not confident that the available information from the EASTROPAC files was adequate regarding the standing stock figures beyond an absolute minimum estimation (G. D. Sharp, P.O. Box 12294, Gainesville, FL 32607, pers. comm.). One should consider that a proportion of the yellowfin forage comprises organisms larger than micronekton, and these prey would be less abundant and less productive than the micronekton. Also, the importance of foraging by other apex predators must be considered.

The population of four dolphin species (*Stenella* spp. and *Delphinus delphis*) is estimated at 7–8 million individuals (R. S. Holt, National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, pers. comm.), and the food consumption of the spotted dolphin (*S. attenuata*) population (3.1–3.5 million individuals) is estimated to be roughly equivalent to that of the yellowfin population (E. F. Vetter, National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, pers. comm.). Thus, food consumption by all four dolphin species could amount to 2 times that of the yellowfin population. Dolphins consume many of the same types of prey as yellowfin (Perrin et al. 1973). We estimate prey consumption by yellowfin to represent less than 33% (100% × (1/(1 + 2))) of the apex predation in this community. The predation rates of other tuna species, billfishes (Istiophoridae and Xiphiidae), dolphinfish (Coryphaenidae), sharks, and seabirds require further investigation before concluding that the food supply is more than adequate.

Conclusions and Implications

The estimates of daily ration for yellowfin tuna derived from the bioenergetics model and tracking study were median among the three independent estimates, lending validity to the use of such models in trophic analyses. The differences between our direct and indirect estimates imply that ration estimates derived from gastric evacuation rates and stomach contents data were too low or that the bioenergetics and cesium budget estimates were too high. The possibility that the bioenergetics model overestimates tuna energy requirements deserves consideration. Metabolic rates of tunas are reported to be 2–3 times higher than in other active fishes swimming at similar speeds (Gooding et al. 1981; Stevens and Dizon 1982; Boggs 1984). Perhaps these findings are due to some bias in the measurement of tuna metabolic rates (due to capture stress, confinement, handling, poor nutrition, starvation, etc.). The independent estimate of energy requirements from stomach contents and gastric evacuation rates indicates that the bioenergetics model could be positively biased by about 30%. This is not enough to account for the major difference between tunas and equally active, cold-bodied fishes. In contrast, the other independent estimate (from cesium concentrations) suggests that the bioenergetics model is not positively biased.

Ration estimates for dominant apex predators and estimates of trophic transfer efficiency are the raw materials required for "top-down" trophic models that can provide estimates of production and biomass for animals at lower trophic levels. Our independent estimates of ration varied above and below the bioenergetics estimate by less than 30%. Direct sampling of forage biomass at sea may be much less precise than estimates based on the "top-down" approach. Direct standing stock estimates such as those of Blackburn et al. (1970) are hampered by gear inadequacies, time limitations, and increasing costs of ship time. Increased understanding of patchy distributions (Fasham 1978; Wormuth and Roper 1983), gear avoidance, and gear selectivity (Kashkin and Parin 1983; Pearcy 1983) suggests that the estimates of Blackburn et al. (1970) may be least accurate for the highly mobile types of prey consumed by yellowfin. Direct sampling must be repetitive to provide more than point estimates whereas trophic models can be dynamic and descriptive of changes at lower levels as a function of the bioenergetics and food habits of the apex predators (Laevastu and Larkins 1981; Stewart et al. 1981). Major apex predators are much more effective than research vessels as samplers of production at intermediate trophic levels.

The "top-down" trophic approach in our study reveals a huge unexploited resource in the form of the frigate tunas in the eastern tropical Pacific. The relationship between frigate tuna production and yellowfin tuna production requires further examination. A more complete trophic analysis could indicate the presence or absence of a food surplus for yellowfin tuna. Such a model will require inputs for the other predators. If adequate estimates for the prey are also found, the analysis can be extended down to the level of primary production and compared with independent estimates, which was done by Adams et al. (1983), Longhurst (1983), and Polovina (1984). At present, there is no compelling evidence for or against food limitation of yellowfin tuna.

The low trophic transfer efficiency between ingestion and production by yellowfin in contrast with their high growth rate, mortality rate, and production to biomass ratio suggests a trophic structure that differs from that of more productive ecosystems. A high production to biomass ratio could be maintained without a high transfer efficiency as long as the ratio between the production of forage and the standing stock of predators is large. In this situation the predator population puts a higher proportion of energy into turnover and maintains a smaller standing stock. This may be characteristic of many tropical pelagic predators that grow rapidly in spite of high metabolic rates in an oligotrophic habitat.

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AGE DEPENDENT FECUNDITY, NUMBER OF SPAWNINGS PER YEAR, SEX RATIO, AND MATURATION STAGES IN NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

Richard H. Parrish,[1] Donna L. Mallicoate,[1] and
Richard A. Klingbeil[2]

ABSTRACT

Maturity stage data from fishery sampling programs and ovarian histological data from research cruises were used to develop a method for determining the age-specific number of spawnings per year and annual fecundity of the central stock of northern anchovy, *Engraulis mordax*.

The sex ratio was found to be size and age dependent in both the fishery and trawl surveys with females increasingly dominant in the larger and older size and age classes. The overall sex ratio in trawl surveys was nearly 1:1; the fishery data favored females 1.48:1. The magnitude and duration of maturity stages were size and age dependent with peak spawning occurring earlier in the season in younger fish. Maturity stages and histological classes with hydrated eggs showed essentially the same diurnal pattern for nightly spawning activity indicating that the presence of hydrated eggs could be used as an index of daily spawning. The daily spawning incidence and total annual fecundity were found to be heavily age dependent. Females in their first spawning season had an average of 5.3 spawnings, while those in their fourth had an average of 23.5 spawnings. When combined with the higher batch fecundity of larger fish this results in 4+ year-old females producing nearly 5 times as many eggs per unit of weight as 1-year-olds. When the age-specific fecundity and sex ratio in the fishery are combined it is apparent that the catch of a ton of 4+ year-old northern anchovy reduces the reproductive potential of the stock 7.3 times as much as the catch of a ton of 1-year-olds.

It was concluded that age-specific fecundity in multiple spawning fishes is of greater significance for management than previously thought. It is also significant that much of the observed variance in stock-recruitment relationships for multiple-spawning fishes may be due to the fact that spawning biomass is a poor index of the egg production and reproductive potential of the stock.

Age-specific variation in life history rates is a major factor in population and management models of exploited fishes, and variation in reproductive effort is of great significance in such models. Size and age-specific batch fecundity estimates have been available for many species for decades, and for species which spawn only once per spawning season these are readily incorporated into models. However it has been impossible to determine the age-specific reproductive effort of species which spawn many times during a spawning season because there has been no way to determine the number of spawnings per year.

Recent research on the histology of the ovaries of northern anchovy, *Engraulis mordax*, and anchoveta, *Engraulis ringens*, suggest that they spawn approximately once a week during peak spawning months (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Alheit et al. 1983; Alheit et al. 1984). Hunter and Leong (1981), in their study of the spawning energetics of the northern anchovy, found that northern anchovy spawn about 20 times per year. Hunter and Leong (1981) and Alheit et al. (1983) suggested that annual fecundity per unit of parental biomass may be highly variable and dependent upon the nutritional state and size structure of the stock.

Potentially the recently developed histological techniques could be utilized to determine age-specific annual fecundity; however, this would be very expensive as it would require a very large data set which would necessarily be stratified by age and time of year. The objectives of this report are 1) to demonstrate a method for combining the high resolution reproductive information from the histology of the ovaries with inexpensive, lower resolution reproductive information derived from resource surveys and fishery sampling programs to determine the age-specific reproductive potential of a multiple spawning species, and 2) to evaluate the gross anatomical maturity stages which have been

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[1] Southwest Fisheries Center, Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, P.O. Box 831, Monterey, CA 93942.

[2] California Department of Fish and Game, 245 W. Broadway Street, Long Beach, CA 90802.

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utilized in field sampling programs for northern anchovy and to use the historical data from these programs in conjunction with ovarian histological data to describe age-dependent annual fecundity in the central stock of northern anchovy.

DATA SOURCES

There are three major sources of biological data for adult northern anchovy in California: samples taken from the commercial fishery (Collins and Spratt 1969), samples taken from midwater trawl hauls carried out by the Sea Survey Program (Mais 1974), and samples taken primarily by midwater trawl during egg production cruises (Picquelle and Hewitt 1983). The first two sources are the result of long-term research and monitoring programs carried out by the California Department of Fish and Game, and the third is the result of research cruises carried out by the National Marine Fisheries Service. The fishery data used in this analysis consist of biological information for 60,661 northern anchovy sampled from the San Pedro purse seine fleet during the period of 1966-80 and 4,904 northern anchovy sampled from the Monterey fleet during 1966-78. All northern anchovy in the fishery samples were aged and nearly all were assigned maturity stages. We used a geographically restricted subset of the 1966-83 sea survey data (lat. 29.5°-34.5°N; 54,457 northern anchovy). Maturity stages were not recorded for males in the sea survey data and age determinations were made on only a portion (19,031) of the fish sampled. In both data sets age determinations were made from otoliths with methods described by Collins and Spratt (1969). The third source of data, provided to us by B. Macewicz[3], consists of histological information for the gonads of 8,672 females sampled during the months of February to April from 1977 to 1984. Age determinations were not made and maturity stages were not taken on these fish.

The gross anatomical maturity stage description used for northern anchovy is a slightly modified version of the system developed by Bowers and Holliday (1961) for herring. The system has seven maturity stages which are primarily based on the portion of the body cavity occupied by the gonads and, in the later stages, by the appearance of translucent eggs or milt (Table 1). Herring are considerably larger than anchovy, and they are generally not considered to be multiple spawners; therefore, there are some difficulties in applying the maturity stages to anchovy. The most obvious problem is that a considerable proportion of the anchovy sampled had gonads so small that sex determinations were not made as they would have required magnification. There was also a small proportion of fish in which physical deterioration made sex determination impossible. The California anchovy fishery is primarily for reduction to fish meal, and the quality of the fish was occasionally very poor when the fish were sampled. Another major difficulty is that it is not possible to distinguish between anchovy gonads that are resting (i.e., stage 2) between multiple spawnings in the same season and those resting between spawning seasons. A comparable problem exists with spent fish (stage 7).

TABLE 1.—The international (Hjort) scale of maturity stages of the gonad. From Bowers and Holliday (1961).

Stage 1:	Virgin individuals: very small sexual organs close under vertebral column; ovaries wine-colored, torpedo-shaped, about 2-3 cm long and 2-3 cm thick, eggs invisible to naked eye; testes whitish or greyish-brown, knife-shaped, 2-3 cm long and 2-3 cm broad.
Stage 2:	Maturing virgins or recovering spents: ovaries somewhat longer than half the length of ventral cavity, about 1 cm diameter, eggs small but visible to naked eye; milt whitish, somewhat bloodshot, of same size as ovaries, but still thin and knife-shaped.
Stage 3:	Sexual organs more swollen, occupying about half of ventral cavity.
Stage 4:	Ovaries and testes occupying almost two thirds of ventral cavity; eggs not transparent, milt whitish, swollen.
Stage 5:	Sexual organs filling ventral cavity; ovaries with some large transparent eggs; milt white, not yet running.
Stage 6:	Roe and milt running (spawning).
Stage 7:	Spents: ovaries slack with residual eggs; testes baggy, bloodshot.

SEX RATIO

Description of the sex ratio in northern anchovy was confounded by the presence of fish for which the sex could not be determined. The relationship between size and the percentage of these unsexed fish is similar for both the commercial purse seine and midwater trawl data. In both data sets, a large percentage of the fish smaller than 100 mm standard length (SL) are of unknown sex, about 10% of the 101-110 mm fish are of unknown sex, and only a small percentage of the fish larger than 110 mm are of unknown sex (Table 2). The percentages of fish with unknown sex at sizes larger than 110 mm in the purse seine data are somewhat higher than those in the midwater trawl data. This is probably due to the occasional occurrences of fish in which the condition was too poor to allow sex identification. The relationship between age and the percentage of unsexed fish is similar to that described for size (Table 2). It should be noted that both data sets are biased towards larger and older fish. The age composition of anchovy in the midwater trawl data is biased because of the fact that otoliths were often not taken when trawl hauls were dominated by young-of-the-year fish (Parrish et al. 1985). The purse seine data contain a much smaller percentage of small or young fish than the midwater trawl data. This is primarily caused by the fact that a 5-in (about 108 mm SL) minimum size limit was in effect for most of the 1966-80 period.

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[3] B. Macewicz, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038, pers. commun August 1984.

To evaluate the seasonal cycle of the occurrence of northern anchovy for which the sex could not be identified, the monthly percentages of females, males, and anchovy with unknown sex were determined by age group for the San Pedro fishery (Fig. 1). In all age groups the minimum percentages of fish which could not be sexed occurred from about January to May in association with the spawning season. Higher percentages occurred both before and after the spawning season, particularly in the first potential spawning season. This implies that a significant percentage of anchovy mature, or at least partially mature, and then reabsorb their gonadal tissue to the point that their gonads are so small that they cannot be sexed without magnification. It also implies that a bias due to the unsexed fish exists. This bias is at a minimum from January to May and it primarily affects the analyses of fish in their first potential spawning season.

Klingbeil (1978) found the female:male ratios of northern anchovy sampled in the Sea Survey Program and in the commercial fishery to be 1.03:1 and 1.60:1 respectively. The additional years of information from these two sources, in our data sets, pro-

TABLE 2.—Proportion of northern anchovies with unknown sex and sex ratio by size (A) and by age (B).

	San Pedro anchovy fishery				Sea survey (lat 29.5°-34.5°N)			
Length (mm)	Unknown sex	Females/male	Mean SL	Number	Unknown sex	Females/male	Mean SL	Number
				A				
61- 70	1.000	—	—	1	0.996	0.00	—	273
71- 80	0.676	0.71	—	37	0.941	0.94	—	597
81- 90	0.437	0.67	—	252	0.810	0.78	—	1,396
91-100	0.283	0.77	—	2,261	0.500	0.84	—	2,208
101-110	0.114	1.06	—	8,684	0.100	0.82	—	2,882
111-120	0.057	1.30	—	17,186	0.016	0.78	—	4,141
121-130	0.029	1.53	—	19,396	0.007	1.07	—	4,016
131-140	0.014	2.10	—	10,010	0.003	1.43	—	2,439
141-150	0.007	2.90	—	2,354	0.003	2.56	—	772
151-160	0.009	4.43	—	438	0.005	3.09	—	185
161 +	0.024	7.20	—	42	0.000	9.67	—	32
Total	0.057	1.48	—	60,661	0.187	1.02	—	19,031
				B				
Age				Annual				
0	0.202	0.83	104.2	1,862	0.779	0.81	88.7	3,616
1	0.090	1.15	112.8	16,167	0.122	0.88	107.2	4,812
2	0.046	1.49	121.1	20,885	0.022	0.86	119.4	4,733
3	0.036	1.76	126.3	14,174	0.010	1.15	126.4	3,543
4 +	0.022	2.01	134.0	7,573	0.003	1.66	135.0	2,327
Total	0.057	1.48	121.2	60,661	0.187	1.02	113.7	19,031
Age				February-April				
0	—	—	—	0	—	—	—	0
1	0.093	0.95	106.5	4,646	0.153	0.79	101.0	2,271
2	0.027	1.33	116.2	4,279	0.004	0.78	117.3	2,035
3	0.018	1.45	123.3	3,410	0.002	1.04	125.3	1,928
4 +	0.014	1.69	134.4	3,620	0.001	1.55	134.6	1,382
Total	0.041	1.30	119.0	15,955	0.048	0.96	117.6	7,616
Age				August-December				
0	0.259	0.77	104.2	1,204	0.831	0.78	88.6	3,216
1	0.083	1.19	117.6	6,411	0.104	0.97	112.2	2,198
2	0.060	1.59	123.1	12,082	0.035	0.91	120.5	2,311
3	0.051	1.92	127.7	7,648	0.021	1.28	128.1	1,255
4 +	0.039	2.33	132.9	2,532	0.007	1.57	135.4	560
Total	0.069	1.58	123.2	29,877	0.316	1.02	109.7	9,540

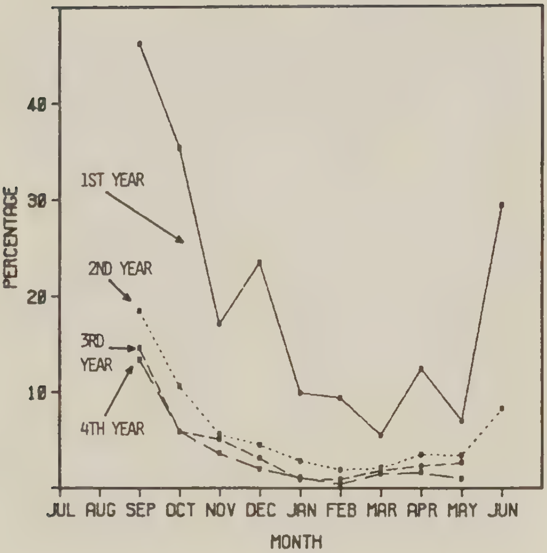

FIGURE 1.—The monthly percentages of northern anchovies with unknown sex, by age group, in samples from the San Pedro fishery.

duced essentially no change in the sex ratio in the sea survey data (1.02:1). However, there was a reduction in the proportion of females in the fishery data (1.48:1) which was associated with a reduction in the average age of anchovy in the catch after 1977 (Mais 1981). Sunada and Silva (1980) also found a female:male sex ratio greater than unity in the northern Baja California purse seine fishery, 2.15:1 in 1976 and 1.44:1 in 1977. Alheit et al. (1984) reported a sex ratio of 1.30:1 in purse seine caught Peruvian anchoveta sampled during their spawning season. Klingbeil (1978) and Alheit et al. (1984) reported that during the spawning season there were unexpectedly large numbers of samples in which sex ratios were heavily dominated by either males or females. Alheit et al. (1984) suggested that "hydrated females segregate, either by depth or area, from the 'normal' school, taking a high percentage of males with them forming 'spawning schools' dominated by males."

Analysis of the sex ratio by size and age groups shows that there are increasingly larger proportions of females in the larger and older groups (Table 2). This trend is evident in both the fishery and sea survey data. In the fishery data there are more males than females identified in the fish smaller than 100 mm SL and in age group 0. The proportion of females increases until there are more than twice as many females as males among fish larger than 130 mm and in age group 4+. There is a similar trend in the sea survey data; however, females do not outnumber males until the fish are larger than 120 mm and 3 yr of age. The sex ratio in age group 4+ is 1.66:1. The apparent dominance of females in the larger size classes may be partially caused by sex related differences in growth rates; however, their dominance in the older age classes of both the purse seine and midwater trawl samples cannot be explained by differences in growth. We grouped our data sets into the spawning months (February-April) and nonspawning months (August-December) in order to evaluate features which might be caused by behavioral differences that may occur during the spawning season. This analysis shows that the overall sex ratio in northern anchovy taken by midwater trawl is close to 1:1 in both nonspawning and spawning seasons (Table 2B). It also shows that the sex ratios in younger fish are dominated by males and those in older fish are dominated by females. The overall sex ratio in northern anchovy sampled in the purse seine fishery is heavily dominated by females; however, the sex ratio is higher in the nonspawning season (1.58:1) than in the spawning season (1.30:1). The crossover from male to female dominance of the sex ratio occurs between age group 2 and 3 in the sea survey data and at age 1 in the fishery data.

MATURITY STAGES IN NORTHERN ANCHOVY

Seasonal Variation in Maturity Stages

To determine which of the various data sets available for northern anchovy were best suited for evaluating maturity stages in the central stock, we examined the seasonality of three grouped maturity stages of four data subsets. The grouped stages included immature or resting females (stages 1 and 2); females just beginning to mature (stage 3); and the highly mature, spawning, and spent females (stages 4-7). The data consisted of two sets of samples from the commercial fishery (Monterey and San Pedro) and the sea survey samples from southern California (lat. 32.5°-34.5°N) and northern Baja California (29.5°-32.5°N).

The seasonal patterns of the grouped maturity stages of females sampled in the San Pedro fishery (Fig. 2A), the sea survey in southern California (Fig. 2B), and the sea survey in northern Baja California (Fig. 2C) are quite similar. The pattern in the Monterey fishery differs from that in the other data sets in that spawning is at the highest levels in April and September (Fig. 2D). It cannot presently be determined if there are one or two peaks of spawning in

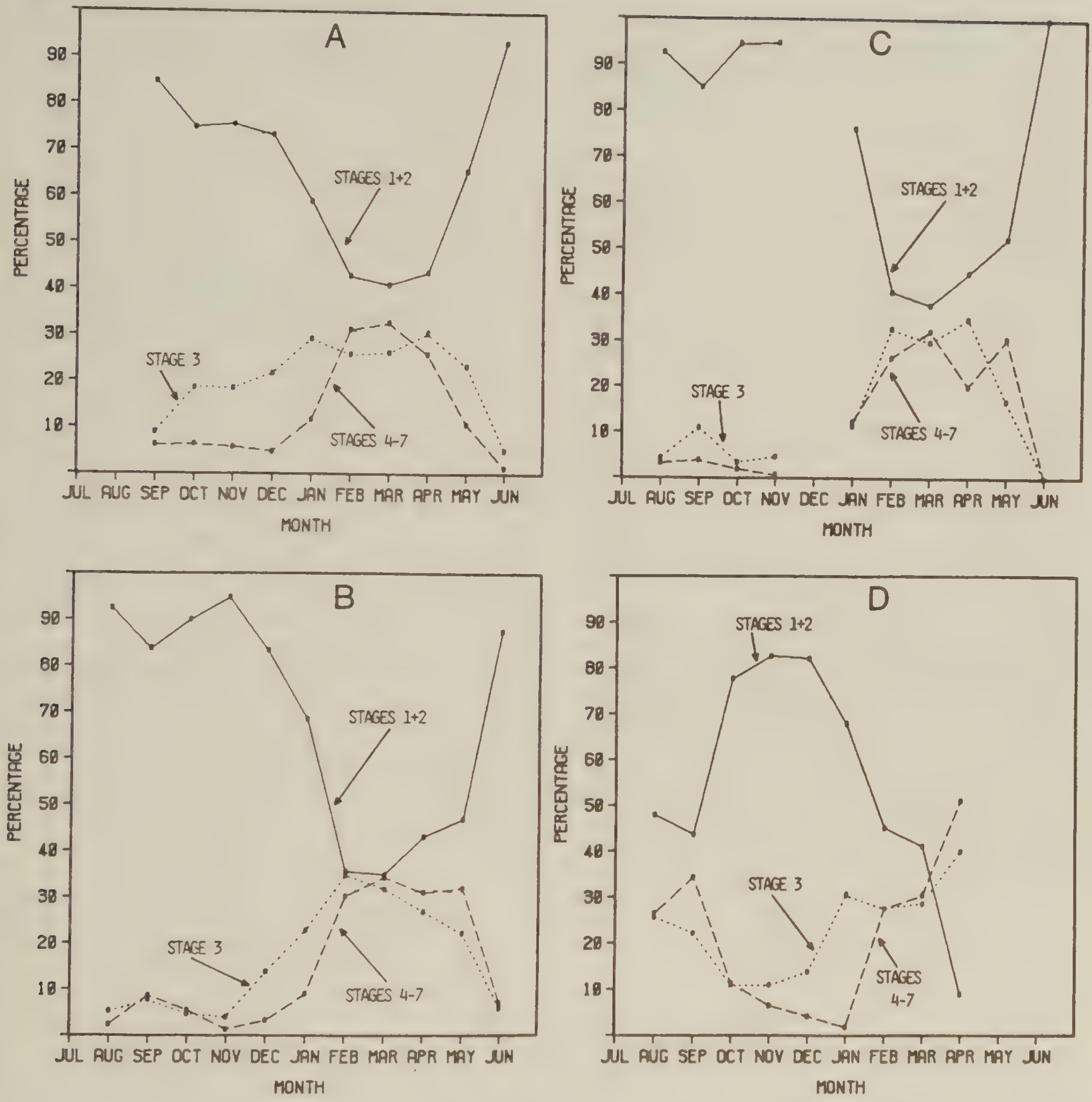

FIGURE 2.—The monthly percentages of grouped maturity stages for female northern anchovies sampled in A, San Pedro fishery; B, Sea survey (lat. 32.5°-34.5°N); C, Sea survey (29.5°-32.5°N); D, Monterey fishery.

the Monterey area due to the lack of data from May to July. Because of the different seasonal pattern of the grouped maturity stages in the Monterey fishery data and because there is more than one stock in this region (Vrooman et al. 1981), it was decided to exclude this area from further analysis. The analyses that follow are based on the combined San Pedro fishery and southern California-northern Baja California sea survey data sets (52,352 females of which 41,930 were aged).

To obtain a first approximation of the magnitude and duration of maturity stages in the central stock of northern anchovy, the monthly percentages of fish with each maturity stage were calculated for females and for males. The seasonal patterns were found to be essentially the same for males and females; however, the males tended to have somewhat larger percentages of fish in the higher maturity stages. Our presentation is limited to information on females.

The proportion of females classified as stage 1, virgin individuals, is at a minimum during the spawning season, comprising <10% of the females sampled during February, March, and April. However, during the summer more than half of the females were classified as stage 1 (Fig. 3A). Stage 2 females, maturing virgins and recovering spents, are at a minimum in August (when most females are classified as stage 1). From September until January between 40 and 60% of the females are classified as stage 2. During the spawning season, and just after, the percentage of stage 2 females dropped between 30 and 40%. The August to September decline in the percentage of stage 1 females is primarily caused by the sharp increase in the proportion of stage 2 females. Thus, the combined percentage of stages 1 and 2 females is probably a reasonable inverse indicator of the seasonality of spawning. However, during the spawning season an unknown proportion of those classified as stages 1 and 2 are females that have recently spawned and are between multiple spawnings.

Stage 3 females (ovary enlarged, occupying about half of the length of the ventral cavity) have a considerably different pattern. There is a gradual increase from about 5% in August to about 30% in January. This percentage is maintained until April, i.e., through the spawning season; it then drops to about 5% in June. The monthly percentages of the higher maturity stages (4, 5, and 6) clearly delineate the spawning season as primarily a January-May event (Fig. 3B). The relatively constant low level of stage 7 females is unexpected as the maximum proportion of spent fish would be expected to occur just after the peak of spawning.

Maturity Stage Relationships with Size and Age

To examine potential relationships between the size and age of northern anchovy and the duration and magnitude of maturity stages we calculated the monthly percentages of grouped maturity stages for four size classes (81-100, 101-120, 121-140, and 141-160 mm SL) and four age groups (1, 2, 3, and 4+). Age group 1 includes fish prior to and after their first potential spawning season (i.e., young-of-the-year fish in July through the following June). Age group 4+ includes fish in their fourth and subsequent spawning seasons. The grouped maturity stages (1, 2, 3, and 4-7) are the same as those presented earlier.

Size has a large effect on both the duration and magnitude of maturity stages in northern anchovy. With the exception of those sampled from February to April nearly all of the 81-100 mm SL females were classified as immature or resting (Fig. 4A). In addition, the majority of this size anchovy have gonads too small to determine their sex without magnification (Table 2). As the size class increases the percentage of stages 1 and 2 decreases; this occurs in all months; however, the minimum percentage of

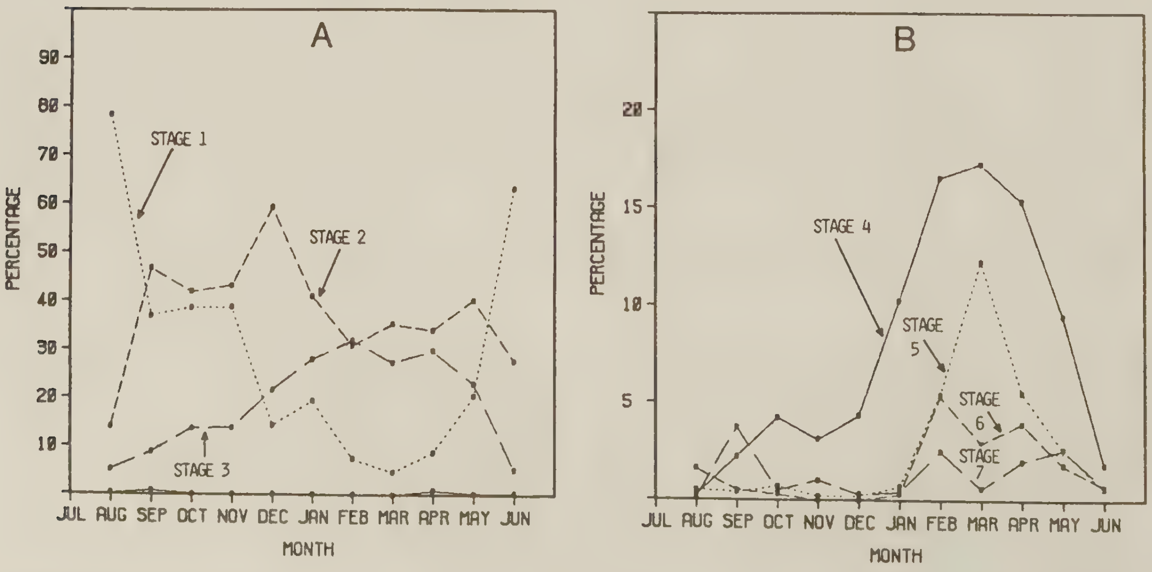

FIGURE 3.—The monthly percentages of individual maturity stages for female northern anchovies. A. Stages 1-3. B. Stages 4-7.

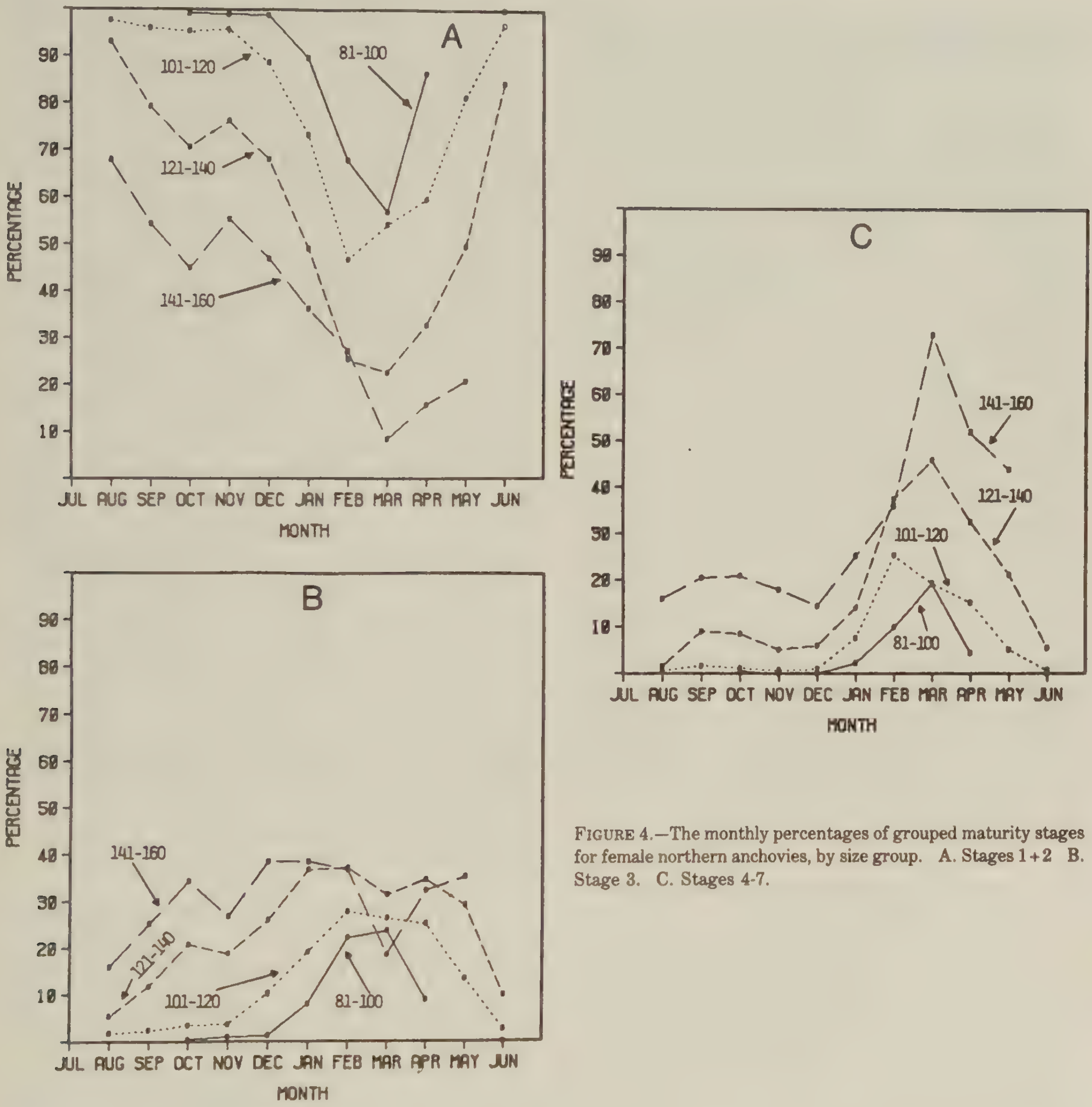

FIGURE 4.—The monthly percentages of grouped maturity stages for female northern anchovies, by size group. A. Stages 1 + 2 B. Stage 3. C. Stages 4-7.

stages 1 + 2 occurs in February to April. The percentage of females just beginning to mature (i.e., stage 3) has an abrupt peak in February-March in the smallest size class (Fig. 4B). This peak becomes increasingly spread out in the larger size classes. The higher maturity stages (4-7) are most abundant from February to April in all size classes (Fig. 4C). The larger size classes have much larger percentages of females in the higher maturity stages than the smaller size classes, and there is a minor peak in the percentage of the higher maturity stages during the fall in the two largest size classes. Analysis of the data by age group showed, as would be expected, that increased age has essentially the same effect as increased size on the magnitude and duration of maturation stages.

SPAWNING INCIDENCE AND FECUNDITY

Studies by Hunter and Goldberg (1980) in California and Alheit et al. (1983) in Peru examined postovulatory follicles to determine the spawning frequency of female anchovies (i.e., the time interval between spawnings). A second method would be to determine the percentage of females with hydrated eggs. Hunter and Macewicz (1980) showed that northern anchovy begin hydrating eggs at about 0600 in the morning and by sunset about 14% of the females have hydrated eggs. They felt that the best indicator of the time of spawning was the occurrence of both hydrated eggs and new postovulatory follicles. This occurred in a low percentage of their samples indicating that spawning was completed rapidly; the time of maximum spawning occurred between 2100 and 0200 with a peak between 2200 and 2300. Hunter and Macewicz (1980) divided the nightly pattern of spawning in anchovy into three periods: "early spawning period (1800 to 2100 hours), some spawning occurs but the ovaries of most reproductively active females are in the hydrated stage; maximum spawning (2100-0200 hours), most females spawn (females with hydrated eggs decline to 0 and females with new postovulatory follicles reach the maximum number for the night); and post-spawning (0200-0600 hours), little or no spawning occurs and females destined to spawn the next night begin hydration." A considerable amount of new histological data is now available as a result of a series of egg production biomass surveys for northern anchovy. B. Macewicz (fn. 3) has analyzed the histology of the ovaries of 8,672 anchovy sampled in these surveys, and our analysis of this new information verifies the temporal patterns which Hunter and Macewicz (1980) described from a much smaller sample (Fig. 5).

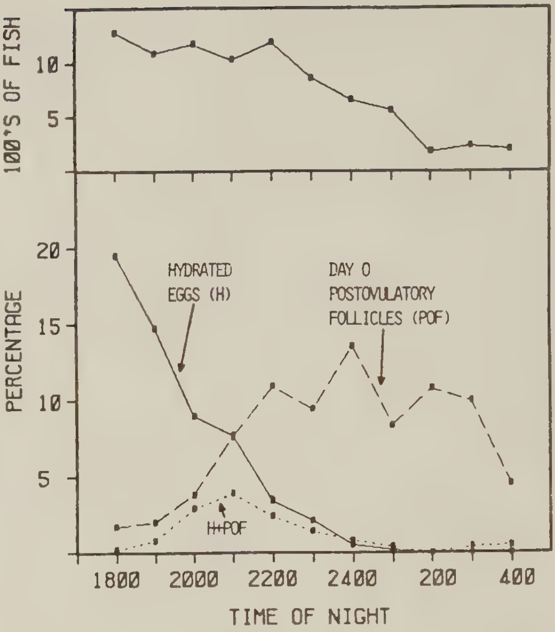

FIGURE 5.—The percentages of female northern anchovies with ovaries in three histological classes, by time of night.

Comparison of Maturity Stages and Histology Classes

The histological data show that during the early evening the percentage of females with hydrated eggs could be an indicator of the percentage of females spawning per day (i.e., the spawning incidence). To use the extensive maturity stage data available for northern anchovy it is necessary to determine the relationships between the histology of the gonads and the maturity stages used in the California Department of Fish and Game's sampling programs. To date histological and field maturity stage data have not been taken on the same individuals; therefore, analysis is limited to comparisons of the two data sets. In the following comparisons the sea survey and histology data sets were limited to samples taken during the period 1977-84 and during the principal spawning season (i.e., February-April). Since nearly all of the trawls were taken at night, the data were limited to those taken from 1800 to 0500 h. The midwater trawl hauls were normally 15 min in duration, and about 30% of the fish in the histological data set and 30% in the maturity stage data sets were taken in the same trawl hauls during cooperative cruises.

The histological data are divided into six classes (B. Macewicz fn. 3):

1. Ovaries with hydrated eggs and no day-0 postovulatory follicles.
2. Ovaries with hydrated eggs and day-0 postovulatory follicles.
3. Ovaries with day-0 postovulatory follicles and no hydrated eggs.
4. Ovaries with day-1 postovulatory follicles.
5. Mature ovaries with no hydrated eggs, no day-0 nor day-1 postovulatory follicles.
6. Immature ovaries, few or no yolked oocytes, no atresia present in the ovary other than late-stage corpora atretica.

Northern anchovy, spawning on the night they were sampled (day 0), include the first three classes; those that spawned on the night before they were sampled (day 1) are class four.

A comparison of the percentages of hydrated females in the sea survey data (i.e., stages 5 + 6) with that in the histological data (i.e., classes 1 + 2) shows that they have essentially the same pattern from the onset of spawning in the early evening until spawning is completed in the early morning (Fig. 6). This implies that in the early evening maturity stages 5 + 6 can be used to estimate the spawning incidence; however, within a few hours after sunset the percentage of females with hydrated eggs (i.e., stages 5 + 6) rapidly becomes an underestimate of the incidence of spawning due to the completion of spawning. If only the females (n = 2,161) sampled between the hours of 1800 and 2000 are considered, then the percentage in maturity stages 5 + 6 (15.3%) is quite close to the percentage of day-0 females calculated for the total histology data set (15.9%).

The variation throughout the night of the percentages of the other maturity stages is also of interest as it offers some insight into the meaning of maturity stages in anchovy. Hunter and Macewicz (1980) showed that spawning primarily occurs between the hours of 1800 and 0200. In the sea survey data the percentage of stages 5 + 6 falls from 15.3 to 1.6% over this time period (Fig. 7). The expected maturity stage that should increase over this time period is stage 7 (i.e., spents: ovaries slack with residual eggs). This, however, is not the case. The percentage of stage-7 females has very little variation over the 1900-0200 period; going from 2% at 1900 to 3.6% at 0200. This suggests that residual eggs occur in only a small percentage of anchovy and that stage 7 cannot be used to determine if an anchovy has spawned within 24 h. This is consistent with Stauffer and Picquelle's (1980) observation that field-spawned northern anchovy were found to release nearly 100% of their hydrated eggs. The percentages of the other maturity stages show considerable variation from 1900 to 0200 h. Stages in which the ovary is small (i.e., 1+2) occur in about 37% of the females in the early evening. This increases rapidly after 2300 and by 0200 these stages comprise about 46% of the females. Stages 3 + 4, in which the ovaries occupy from one half to two thirds of the ventral cavity, occur in about 46% of females in the early evening. This rises to a peak of about 54% at 2300-2400 and then declines to about 49% at 0200.

Our interpretation of the patterns exhibited by the sea survey data is that the percentage of females at stages 5 + 6 in the early evening (i.e., 15.3%) is a valid estimate of the percentage of sampled females with hydrated eggs. However, as the night progresses the percentage of stages 5 + 6 declines. At the peak of spawning, just before midnight, many females appear to be misidentified as stages 3 + 4. This could occur if they had spawned part of their eggs before they were captured and if the person making the maturity stage determinations used the size of the ovary, rather than the presence of hydrated eggs, to determine the maturity stage. After midnight an increasing percentage of spawning females have

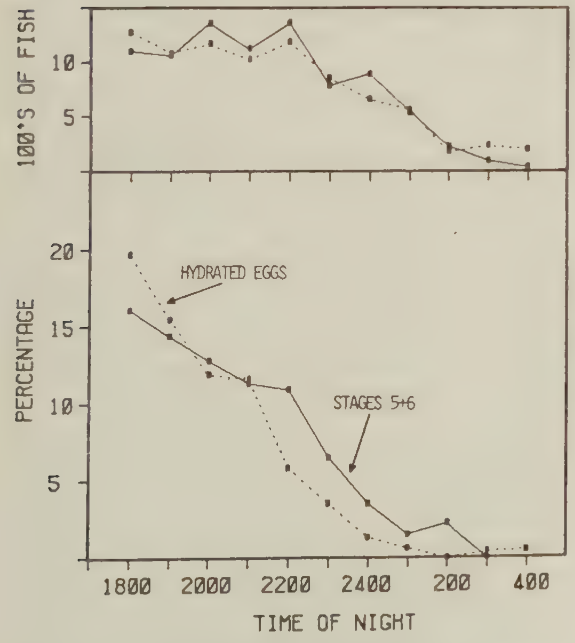

FIGURE 6.—The percentages of female northern anchovies with hydrated eggs and with maturity stages 5+6, by time of night.

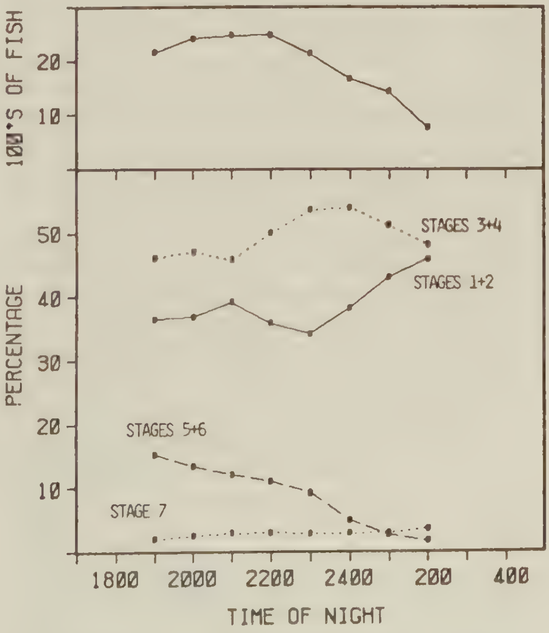

FIGURE 7.—The percentages of grouped maturity stages for female northern anchovies by time of night. (Two hour moving average.)

apparently spawned all of their hydrated eggs and they are then classified as stage 1 or 2. The meaning of stage 7 in female anchovy remains a mystery.

The seasonal and diurnal patterns described above indicate that, with the exception of stages defined by the presence of hydrated eggs, gross anatomical maturity stages have little utility other than describing the seasonality of spawning. However, field identifications of the presence of hydrated eggs, if they are calibrated with histological data and if the diurnal pattern of hydration is known, can potentially be used to determine spawning incidence.

Several authors have pointed out that females with hydrated eggs and actively spawning females were more numerous than females with day-1 postovulatory follicles, and have suggested that hydrated and actively spawning females may be more susceptible to capture due to behavioral or physiological factors (Hunter and Goldberg 1980; Stauffer and Picquelle 1980; Alheit et al. 1984). Previous workers have therefore used the percentage of day-1 females as the index of the daily spawning incidence. The overall percentages of day-0 and day-1 females in the histology data set (8,672 females) used in our analyses are 15.9 and 11.5%. Alheit et al. (1983) found the overall percentages of day-1 and day-2 Peruvian anchoveta females to be 17.26 and 14.81%. Hunter and Goldberg (1980), and subsequent workers on the northern anchovy, took their samples at night whereas Alheit et al. (1983) took their Peruvian anchoveta samples primarily during the day. Therefore the definition of day-1 is somewhat different in studies of the two species. In our analysis both day-0 and day-1 females appear to be more susceptible to capture by midwater trawl in the early evening than later at night. The percentages of both decline as the night progresses; however, the decline is more extreme in the day-0 females (Fig. 8).

The use of maturity stages 5 + 6 could result in several sources of bias that would tend to produce overestimates of the spawning incidence of northern anchovy. If females with hydrated eggs are more susceptible to capture, there will be a tendency to produce biased estimates. However, this bias would not be expected to be size or age dependent, nor would it be expected to vary during the spawning season. The same bias would be expected to occur in 1- and 4-yr-old hydrated females and the same bias would be expected in February and April. Therefore the use of the percentages of hydrated females or maturity stages 5 + 6 females may result in overestimates of the total spawning incidence or annual fecundity, but the relative spawning incidence or relative annual fecundity of the different age groups would not be biased. A second source of bias is that an unknown number of females have ovaries so small that visual determination of sex is impossible without magnification. Therefore, the incidence of spawning is overestimated because it is calculated by dividing the number of stages 5 + 6 females by less than the total number of females. This bias is size and age dependent, being much more common in smaller and younger anchovy, but not month dependent. Note that the various studies of the spawning incidence in northern anchovy and Peruvian anchoveta have defined the spawning incidence to be the number of females spawning per day divided by the number of *mature* females, i.e., these studies exclude immature females, which are primarily the smaller and younger fish, from the calculation.

There are also several sources of bias that would tend to produce underestimates of the spawning incidence. The anchovy fishery in southern California primarily occurs at night during the fall months and during the daylight hours in the spring. A period of low availability to the commercial fishery is associated with the spawning season. Mais (1974) associated this phenomenon with variation in schooling behavior and showed that acoustic surveys detect relatively few "commercial-sized" anchovy schools during the spawning season. If low availability to the commercial fishery is associated with spawning ac-

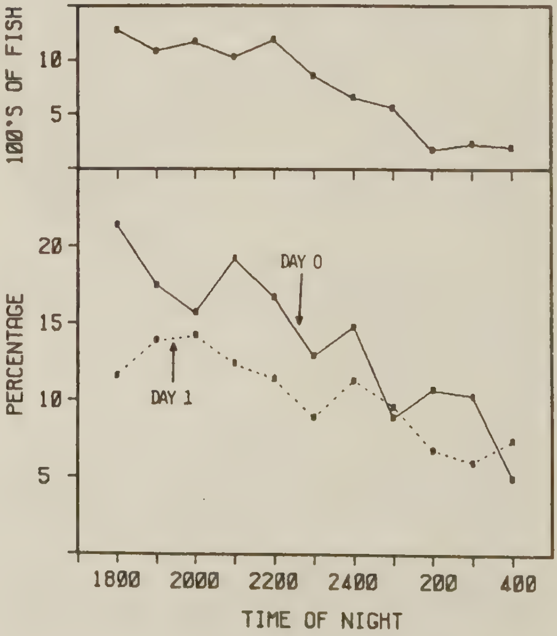

FIGURE 8.—The percentages of day-0 and day-1 female northern anchovies by time of night.

tivity, it is probable that the fishery undersamples the active spawners. In addition, a proportion of the commercial catches occur during the time of day when the females do not have hydrated eggs. The fishery data will therefore tend to underestimate the spawning incidence. The total sea survey data will also produce an underestimate as it includes samples taken throughout the night.

The combined fishery-sea survey data used in our analyses will therefore provide only an index of the daily spawning incidence. To evaluate the potential net bias of this index we calculated the percentage of females with maturity stages 5 + 6, in the combined fishery-sea survey data, and the percentage of females with day-1 postovulatory follicles, in the histological data. To make the data comparable we used the period 1977-84 and the months February-April. The percentage of females with maturity stages 5 + 6 and the percentage of females with day-1 postovulatory follicles was 10.9 and 11.5%. Use of the maturity stage data will therefore slightly underestimate the daily spawning incidence (i.e., 10.9/11.5 = 0.948).

Size Dependent Batch Fecundity

Annual fecundity in the northern anchovy is dependent upon the batch fecundity and the number of spawnings per year. Batch fecundity is size dependent and the best average estimate over six seasons (Hunter et al. 1985) is given below. Note that Hunter et al. found significant variation (ANOVA) among years.

$$\text{batch fecundity} = -1{,}104 + 614\ (\text{WT})$$

where WT = female wet weight, minus ovaries, in grams. During the spawning season ovary free weight of northern anchovy is equal to 95% of the total wet weight (Hunter and Leong 1981). Batch fecundity, with the above relationships, for a typical 1-yr-old (12 g) and a typical 4-yr-old (24 g) are 5,896 eggs and 12,895 eggs. On a per unit weight basis the 24 g fish would produce only 9.4% more eggs than the 12 g fish. Age-dependent variations in batch fecundity are therefore of only minor significance in the relationship between spawning biomass and annual fecundity. There is the possibility that batch fecundity could vary over the spawning season, and since we have shown an age-dependent seasonality in the spawning incidence of northern anchovy, this could potentially contribute to age-dependent differences in annual fecundity. Hunter and Leong (1981), however, found average batch fecundity to be essentially the same in samples taken in January-February and in March-April.

Size-Dependent Histology Classes

Hunter and Macewicz (1980) found no relationship between size and the percentage of mature female northern anchovy with day-1 postovulatory follicles. Later work by Picquelle and Hewitt (1984) showed that weight and spawning incidence were highly correlated in the northern portion of the central stocks range. They stated that this implied that the larger females spawned more frequently or that the smaller females had a much shorter spawning season. We analyzed the larger histology data set now available and found that the percentages of females with hydrated oocytes or with day-1 postovulatory follicles, as well as the percentage of females with maturity stages 5 + 6, were dependent upon the size of the females (Fig. 9).

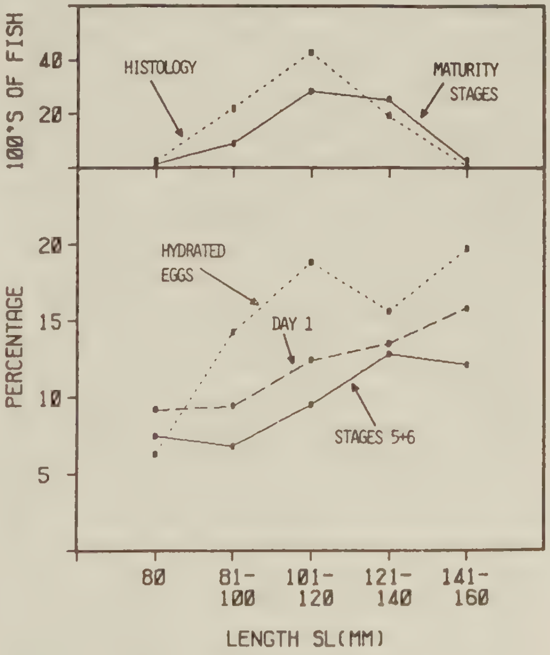

FIGURE 9.—The percentages of female northern anchovies with hydrated eggs, with maturity stages 5 + 6, and day-1 histological classes by size group.

Age-Dependent Spawning Incidence and Annual Fecundity

To assess age-dependent, annual fecundity in the central stock of northern anchovy we calculated the number of spawnings and the fecundity on a monthly basis for age groups 1, 2, 3, and 4+. Average monthly wet weight by age was taken from Mallicoate and Parrish (1981). The number of spawnings per month was calculated from the number of days per month and the index of daily spawning (i.e., the proportion of stages 5 + 6). Note that the bias due to the unknown sex problem discussed earlier would tend to cause an overestimation of the daily spawning incidence: particularly in females in their first spawning season. Also note that the index of daily spawning underestimates the spawning incidence by about 5%.

Our analysis shows that there are large, age-dependent variations in the proportions of female northern anchovy spawning as the spawning season progresses (Fig. 10). From July until January all age groups have a very low daily spawning index. Intensive spawning commences in February and all age groups have roughly the same spawning index (9-12%). In March the spawning index of age group 1 declines to about 2%; it increases slightly in April and declines to about 1% in May. In age group 2 the spawning index increases to 13% in March and then declines to about 2% by May. Age groups 3 and 4+ have peak spawning indices in March (25 and 27%), considerable spawning in April (10 and 17%) and lesser amounts in May (3 and 6%) and June (3 and 6%).

Older females have a much larger number of spawnings per spawning season than younger females (Table 3). In their first spawning season females have an average of 5.3 spawnings. In their second spawning season this rises to 11.9 and in their third and fourth plus seasons the number of spawnings rises to 19.2 and 23.5. The increase in the number of spawnings associated with increasing age appears to be primarily due to the increase in the length of the spawning season that occurs in older fish. The average number of spawnings per season for all females sampled was 15.1. This is less than the estimate that Hunter and Leong (1981) developed from the energetics of female northern anchovy (i.e., 20 spawnings per year). Their calculations indicated that mature female northern anchovy spawned on the average 15 times between February and September; their calculation of the number of spawnings from October to January (5) was estimated indirectly from the relative monthly larval abundance in 1953-60. Our estimate of the number of spawnings from February to September (14.3) is very close to the Hunter and Leong (1981) estimate which was based on a smaller histology data set. However, our estimate of the number of spawnings from October to January is only 0.8 and is much less than their indirect estimate based on the relative seasonal larval abundance for the 1953-60 period. The central stock of northern anchovy was at a much smaller population size in 1953-60 than it was in 1966-84 (MacCall 1980) and northern fish, with a seasonal spawning pattern similar to that occurring in the Monterey data, may have comprised a larger proportion of the anchovy population off California during the 1953-60 period than at present thus inflating Hunter and Leong's estimate for the October-January period.

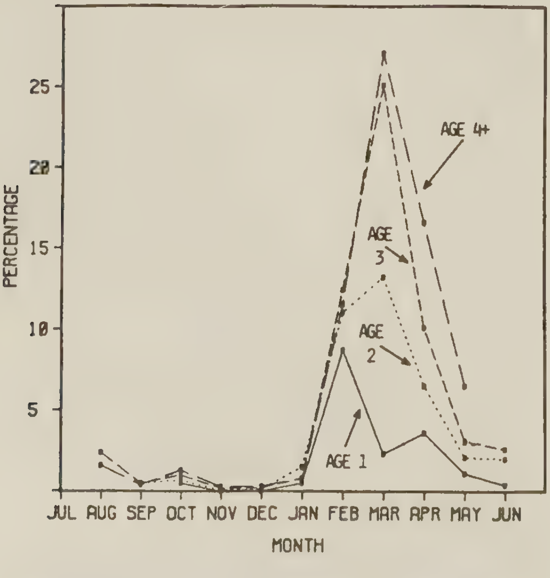

FIGURE 10.—The monthly percentages of female northern anchovies with maturity stages 5+6, by age group.

Our analysis indicates that annual fecundity in the central stock of northern anchovy is heavily age dependent; the average 4+ yr-old female produces nearly 10 times as many eggs as a 1-yr-old female (Table 3). Our calculations show that central stock, female anchovy produce 2,803, 6,550, 11,434, and 13,861 eggs/g of body weight per spawning season in their 1st, 2d, 3d, and 4th plus spawning seasons. Females 4 yr of age and older produce nearly 5 times as many eggs per unit of weight as 1-yr-olds.

DISCUSSION

Over the last decade it has become apparent that recruitment failure is the major threat to many of the world's largest fisheries. In addition, variation in recruitment is a significant causal factor in the interyear variation of the annual catches of many fisheries. Stocks of small pelagic fishes appear to

TABLE 3.—Proportion of maturity stages 5 + 6, number of spawnings and fecundity of female northern anchovies sampled in the Sea Survey Program (lat. 29.5°-34.5°N) and San Pedro fishery.

	July[1]	Aug.[1]	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total[2]	Eggs/g[3]
First spawning season														
Prop. 5 + 6	0.000	0.000	0.000	0.005	0.000	0.000	0.005	0.087	0.023	0.036	0.011	0.004		
Spawnings	0.000	0.000	0.000	0.155	0.000	0.000	0.155	2.436	0.713	1.080	0.341	0.120	5.3	
Wt. (g)	—	—	11.2	11.1	12.0	11.0	11.4	11.6	12.8	13.7	15.4	13.6		
No. eggs	0	0	0	832	0	0	860	13,793	4,536	7,438	2,687	819	32,514	2,803
Second spawning season														
Prop 5 + 6	0.002	0.000	0.005	0.007	0.001	0.001	0.015	0.110	0.132	0.065	0.021	0.020		
Spawnings	0.062	0.000	0.150	0.217	0.030	0.031	0.465	3.080	4.092	1.950	0.651	0.600	11.9	
Wt. (g)	15.5	15.5	17.4	16.8	17.2	16.3	16.2	15.6	16.5	17.7	18.3	17.5		
No. eggs	492	0	1,357	1,887	268	261	8,881	24,626	34,866	17,980	6,230	5,462	102,174	6,550
Third spawning season														
Prop. 5 + 6	0.022	0.024	0.005	0.010	0.002	0.002	0.008	0.124	0.251	0.101	0.031	0.026		
Spawnings	0.682	0.744	0.150	0.310	0.060	0.062	0.248	3.472	7.781	3.030	0.961	0.780	19.2	
Wt. (g)	18.3	18.3	19.1	19.3	19.2	19.3	19.1	18.0	20.7	22.2	20.9	22.7		
No. eggs	6,527	7,120	1,506	3,148	606	630	2,489	33,836	85,360	35,891	10,655	9,467	205,819	11,434
Fourth-plus spawning seasons														
Prop. 5 + 6	0.021	0.016	0.004	0.013	0.003	0.003	0.008	0.115	0.271	0.166	0.065	0.056		
Spawnings	0.651	0.496	0.120	0.403	0.090	0.093	0.248	3.220	8.401	4.980	2.015	1.680	23.5	
Wt. (g)	20.1	20.1	20.9	21.8	22.3	22.2	23.6	23.3	26.6	26.5	25.7	25.7		
No. eggs	6,914	5,268	1,330	4,680	1,071	1,102	2,952	37,390	110,293	67,123	26,454	18,136	322,957	13,861
All spawning seasons combined														
Prop. 5 + 6	0.017	0.021	0.008	0.011	0.002	0.002	0.010	0.107	0.151	0.094	0.044	0.012		
Spawnings	0.527	0.651	0.240	0.341	0.060	0.062	0.310	2.996	4.681	2.820	1.364	0.360	15.1	

[1] Missing data estimated from adjacent months.

[2] Includes 5% correction for spawning incidence bias.

[3] Total eggs/February weight.

be particularly susceptible to collapse; however, perturbations of recruitment is a potential threat to any fishery in which one or two year classes comprise the bulk of the landings. The stock-recruitment approach to understanding or predicting recruitment has fallen into disfavor, at least in the small pelagic fishes, because stock size has not proven to be a good predictor of recruitment. In its pure form (Beverton and Holt 1957; Cushing 1971; Ricker 1975) the stock-recruitment concept is based on two factors: 1) Parent stock size is a measure of the reproductive potential of the stock, and 2) there are compensatory mechanisms which reduce the number of recruits per spawner as the size of the parent stock increases. This compensation occurs through some mix of reduced fecundity of the parent stock, reduced growth of the recruiting cohort and increased mortality of the recruiting cohort. Recruitment variations are usually attributed to changes in environmental conditions, usually unknown, and the causal mechanisms, also usually unknown, are thought to occur during the early life history stages. The present emphasis of recruitment research is on the growth and mortality of the early life history stages. Potential variations of stock fecundity as a factor in recruitment variations has largely been ignored.

There are now 6 years of egg production estimates available for the central stock of northern anchovy (Bindman 1985). The mean spawning incidence for these years is 0.124 and the spawning incidence varied from 0.094 in the El Niño year of 1983 to 0.160 in 1984. This implies that the central stock produced 70% more eggs, per unit of spawning biomass, in 1984 than in 1983. Santander (1980) showed that the Peruvian anchoveta had both reduced spawning and an alteration of the seasonality of spawning during the 1972 El Niño. The results presented here, which show that fecundity is strongly age dependent, suggest that the reduction in age composition caused by heavy exploitation will greatly reduce the average fecundity per unit of biomass and also result in a reduction in the length of the spawning season. It appears that interyear variations in the age composition of a stock or in environmental factors associated with energy reserves or egg production are likely to alter greatly a stock's reproductive potential. If this is the case in other species which have multiple spawning, much of the variance in the stock-recruitment relationships of these fishes may be due to the fact that spawning biomass is a poor index of the reproductive potential of the stock.

To date information concerning age-specific reproductive potential has not been available for multiple spawning fishes because of the difficulty of determining the number of spawnings per year. The pioneering work by Hunter and Goldberg (1980) and later studies based on this work clearly demonstrate that, at least for many clupeids, the spawning incidence or spawning frequency can be determined with properly designed histological studies. Unfortunately a research program designed to determine age-specific reproductive potential would be very expensive as it would require a field sampling progam extending over the whole spawning season, in many cases the entire year; and it would require histological analysis and aging of a large number of females, both quite labor intensive.

It appears that the only way it may be possible to determine age-specific reproductive potential for many fishes is to use the approach developed here which combines two methodologies: histological assessment of ovaries because it unambiguously and accurately measure spawning rate and a traditional fishery sampling program which utilizes an inexpensive rapid index of reproductive condition, such as the maturity stage system or a gonado-somatic index, in which thousands of specimens can be processed. Whichever anatomical grading system is used, its principal purpose would be to determine the percentage of hydrated females. Most of the maturity stages (i.e., 1-4, 7) in the system used for northern anchovy are only of value in describing the seasonality of spawning. The only stages (i.e., 5 and 6) which can be used to determine the number of spawnings are those in which the eggs are hydrated, and they can be directly used as an index in northern anchovy because it is known that the duration of hydrated eggs in the ovary is <24 h. The traditional fishery sampling program may, as in the case for northern anchovy, already be available. If this is the case the principal work will be to calibrate properly the maturity stage or gonado-somatic index with the histological analysis. For this approach to work the fishery must, of course, take hydrated females.

CONCLUSIONS

It is important for those managing fisheries which are susceptible to recruitment overfishing to realize that the alteration in the age structure of a stock that occurs under heavy exploitation may have greater effects on the total fecundity and seasonality of spawning than previously recognized. Management strategies which decrease the exploitation of older, more fecund females could increase yields and also provide increased protection against recruitment overfishing. In northern anchovy there is the additional factor that the sex ratio in the fishery is age dependent (i.e., the female:male ratio for 1-yr-old anchovy in the San Pedro fishery is 0.83:1, whereas that for 4+ yr-olds is 2.01:1). When this factor is multiplied by the difference in the fecundity of the two age groups, it is apparent that the catch of a ton of 4+ yr-old northern anchovy reduces the reproductive potential of the stock 7.3 times as much as the catch of a ton of 1-yr-old fish.

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Investigation of the Cetacean Fauna and Former Dolphin Fishery of St. Helena

Grant Recipient: William F. Perrin, Southwest Fisheries Center, National Oceanic and Atmospheric Administration, La Jolla, California.[1]

Grant 2543: To determine the identity of dolphins taken in a former fishery and to investigate historic methods, landings, and present status of the fishery.

The cetacean fauna of St. Helena has been very poorly known scientifically. Melliss (1875) described "five kinds of cetaceous animals commonly known[:] . . . *B. mysticetus* (right whale?) . . . , *P. macrocephalus* (sperm whale) . . . , Delphinus, Linn. . . . one kind only of Dolphin . . . , Phocaena, Linn. . . . two kinds of porpoise . . . Right Whale Porpoise and the Sperm Whale Porpoise . . . ." No further accounts of the cetaceans inhabiting the waters around St. Helena have been published.

Determining the identity of dolphins taken in a small harpoon fishery at St. Helena is important to an ongoing taxonomic study of the dolphins of the genus *Stenella* of the Atlantic. Spotted dolphins in the Atlantic have been referred to in recent years as *Stenella frontalis, S. attenuata, S. plagiodon, S. capensis,* and *S. dubia.* The holotype specimens of all these nominal species consist of skulls only. Unfortunately, our emerging picture of the two apparently valid species shows them to differ markedly not in skull characteristics but in color pattern and vertebral count, data not available for the holotype specimens. To solve this problem we plan to gather skull measurements from all available specimens that are referable to one or the other of the two species based on color patterns or vertebral count, to construct discriminant functions (an analytical technique involving simultaneous consideration of a large number of variables), and finally to apply the discriminant function to the holotype specimens, so that they (and the names they carry) can be assigned to one or the other of the species.

For one of the species, an endemic form to which the name *S. plagiodon* has been most commonly applied, there are a large number of fully documented specimens in museums in the United States. Atlantic specimens of the second species, a pantropical form most recently called *S. attenuata* or *S. frontalis*, are much less abundant. We have located only 16 with data on coloration or vertebral count. However, the British Museum has 41 skulls of spotted dolphins taken from St. Helena by local fishermen, mostly in the late 1950s. The skulls came without information on coloration or skeleton but exhibit very low variation, indicating they are all of a single species. The one (ventral) photograph of a St. Helena dolphin in the British Museum Archives shows a color pattern more consistent with that of the pantropical species than with the Atlantic endemic species, but the angle of the photograph prohibits a firm conclusion. We hoped color pattern would identify the type of dolphin taken by the fishermen in St. Helena. If it proved to be the pantropical species, then the large series of skulls in the British Museum could be used in the discriminant analyses aimed at resolving the taxonomic problem.

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[1] Marilyn J. Perrin assisted the grant recipient on this project.

RESEARCH

We observed and photographed dolphins on the lee side of the island from an open fishing boat on five days between May 5 and June 2, 1983. Our usual observation strategy was to make multiple passes through a moving school, taking photographs on the down-swell legs. On May 5 and 26, we observed and photographed the animals underwater.

On May 25, we sailed around the island to observe cetaceans on the south side. However, the weather was very rough, and we saw no cetaceans.

We tape-recorded interviews with 10 fishermen and 1 boat owner concerning the history, methods, catches, and economics of the dolphin fishery, and had more informal discussions with an additional 35 to 40 individuals, including government officials and employees of the St. Helena Fisheries Corporation. We asked for information on the dolphin fishery through a notice in the island newspaper and on a local radio broadcast. We spent several days scanning and abstracting information from books, official records, and 19th-century newspaper files maintained in the island library and archives. Because of lack of time, we examined only a fraction of the material in the archives.

CETACEAN FAUNA

PANTROPICAL SPOTTED DOLPHIN, *STENELLA* SP.

This was the dolphin most commonly harpooned in the fishery. Island fishermen call it "bottlenose porpoise" or simply "porpoise." The skulls in the British Museum are of this species. We clearly observed diagnostic color-pattern characteristics: white-tipped beak, well-defined cape passing high over the eye and with greatest depth at the level of the dorsal fin, narrow light band subsidiary to the cape, flipper stripe to gape, and dorsoventral division of the peduncle into upper dark and lower light areas. Calves are unspotted, and juveniles have pronounced dark spots below. Dorsal spotting in adults is so poorly developed as to appear absent when the animals are seen at a distance of a few meters.

The school that we observed consisted of several hundred dolphins. It came into shallow water within 0.5 km of shore along the southern half of the lee side of the island in the early morning and moved slowly north and headed back offshore at the northern lee edge before noon. During this slow passage the school appeared to be loosely organized and dispersed over a distance of about 0.5 km in subgroups of about 5 to 10 animals. Groups milled, briefly reversed direction, and made short forays offshore. Aerial activity, including high leaps (mostly by juveniles), forward flips, pitch-poling, and tail lobbing, was extensive. Occasional intense flurries of surface activity involving two or more animals was evidenced by violent, confused splashing.

On each occasion as we approached the school, individual dolphins came to meet the boat and rode the bow briefly. They did not surface at the bow to breathe, but moved a few meters away from the boat, blew, and returned to the bow underwater. This differs from typical bow-riding behavior, in which the animals surface to breathe at the bow, and may be related to the fishermen's practice of harpooning dolphins from the bow.

On one day we followed the dolphins to the edge of the lee, where part of the school spent several minutes "surfing" in short steep swells. Some of the dolphins made several passes in the waves, doubling back after traveling 100 m or so.

Fishermen told us that once the school goes offshore, out of the lee of the island, it breaks into several smaller schools. These may be encountered several kilometers offshore in the afternoon. They are occasionally seen on the weather side of the island. Fishermen also said that dolphins are "easiest to find" in April and May.

BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*

This dolphin is called "cowfish" or "cow porpoise," but some fishermen also call it "angerine." It was taken in the fishery in lesser numbers than the spotted dolphin. Several skulls of this species are in the British Museum.

We observed this dolphin at least twice. On May 5, we saw several large dark dolphins with high falcate dorsal fins in the school of spotted dolphins. The fishermen called these cowfish; but we did not get a good look at them. On June 2, we encountered and photographed a small school (10 to 15) of bottlenose dolphins at 0830 hours. As we approached, the animals evaded us by diving for several minutes and coming up about 200 m away. We identified them by their size, coloration, size and shape of dorsal fin, and shape of the head (a short beak sharply demarcated from the melon). On June 5 at 1420 hours, as we left the island, several bottlenose dolphins joined the ship 5 to 7 km offshore and rode the bow and stern wakes for about 10 minutes.

Fishermen told us that cowfish sometimes frequent James Bay at night, feeding on flying fish attracted to lights on the waterfront.

An officer on the R.M.S. *Centaur* showed us a videotape of several bottlenose dolphins riding the bow of the ship just off Ascension Island, about 700 nm northwest of St. Helena, on March 12, 1983.

OTHER SPECIES

Only two species other than spotted and bottlenose dolphins can be said with certitude to occur (or have occurred) at or near St. Helena: the humpback whale and the spinner dolphin, *Stenella longirostris.* Inclusion of the spinner dolphin is based on a skull in the Cleveland Museum of Natural History (No. 2413) labeled as collected at St. Helena by the Blossom South Atlantic Expedition on October 10, 1926. Fishermen to whom we talked did not recognize photographs of spinner dolphins nor did they remember having seen its distinctive spinning behavior. The inclusion of the humpback in the fauna is based on 19th-century newspaper and whaling accounts.

Fishermen told us of a seasonal occurrence or past strandings of several kinds of large whales which they called "humpback," "sperm," "blue," or "right whales," but these reports are not confirmed by specimens or photographs. They also reported occasional or seasonal occurrence of "whale killers," "blackfish," "whitebelly porpoise," and "black porpoise" with blunt heads.

While some of the fishermen use angerine (or "angeline") when referring to the bottlenose dolphin, most use this term to refer to a quite different animal. Our most reliable and conservative informant, a retired fisherman, described the angerine as a little larger than a cow porpoise (which he has measured up to 8 ft long), dark above and cream-colored below, with a few (four to five) white spots on each side and a short beak. He said the animal occurs in groups of a dozen or so, never in the company of other dolphins. Others described the angerine as larger than the cowfish and with a few spots (pink or white and about an inch in diameter) and a white or pinkish belly. Murphy (1947) reported that whalemen used the term "algerine" (possibly derived from "Algerian") for small beaked whales of the genus *Mesoplodon,* but it is very unlikely that this is the usage at St. Helena. The descriptions are most consistent with characteristics of the rough-toothed dolphin, *Steno bredanensis;* however, this is a highly tentative conclusion. The angerine was only rarely harpooned by the islanders and is said to fight harder than other porpoise.

The inclusion by Melliss of the right whale dolphin *(Lissodelphis peronii)* in the fauna of St. Helena seems questionable, as it is a cool-temperate species and the waters around St. Helena are tropical, albeit seasonally verging on warm-temperate.

Dolphin Fishery

A fuller account of the dolphin fishery will be submitted to the Scientific Committee of the International Whaling Commission.

The dolphin fishery likely had its origins in 19th-century whaling; the whalemen harpooned dolphins for practice and for consumption by the crew. This thesis is supported by the islanders' use of Yankee whaling terms such as porpoise, cowfish, algerine, blackfish, and "iron" (for harpoon), and by the implements used in the fishery, which until the 1960s were modeled on sperm-whaling gear.

The pursuit of dolphins has always been an adjunct to other fishing activities. Typically, a dolphin or two was harpooned on the way home from the tuna-fishing grounds after a day of low tuna catch. Before World War II, sails were used. In the 1950s and 1960s the boats converted to small diesel engines, which made catching dolphins easier. A very few bottlenose dolphins were harpooned in the harbor at night. Average annual catches before 1979, when the taking of dolphins was banned, were on the order of 100 to 200 spotted dolphins and 5 to 15 bottlenose dolphins a year, perhaps peaking in the 1950s. Records of landed dolphins sold to the Fisheries Corporation were only kept for 1978, when 37 dolphins were logged (some landed dolphins were not sold to the Corporation). As recalled by the fishermen, the usual daily take by a boat was one or two dolphins. Dolphin meat was highly esteemed, and, when available, brought about the same price as tuna. Despite the ban, a few dolphins (perhaps 5 to 10 annually) are still taken for consumption by boat crews or family use; but dolphin meat no longer appears in the market.

Acknowledgments

We received abundant help, encouragement, and hospitality from the following people in St. Helena (in roughly the order that we met them): Brian and Katherine Sellwood, Basil George, Patrick Joshua, Laurie and Joan Baker, David Harrison, Joan Buckley, John and Silvia Clifford, Miriam Henry, Phillip Dale, Graham Sim, William Lawrence,

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William F. Perrin
Marilyn J. Perrin

8677

CORRECTIONS FOR THE LISTINGS OF THE ECOPATH MODEL

by
J.J. Polovina
Southwest Fisheries Center
Honolulu Laboratory
National Marine Fisheries Service
NOAA, Honolulu, Hawaii 96812, U.S.A.

Network members Drs. D. Pauly and E. Ursin kindly brought to my attention some problems they had with their versions of ECOPATH (see Polovina 1984a, b; Polovina and Ow 1983), particularly when they entered more than one "initial biomass" value. Also, they did not know what ECOPATH actually does with these "excess biomasses".

I made several runs and found that when an excess of biomasses were fixed, two problems arose. In one case a variable was not being completely re-initialized with each new run and in the other case an "if statement" needs to be added to handle the case when a biomass is fixed and there are catch data present for the same species group. Corrections for the listings in Polovina and Ow (1983) are given in the box below.

When there are k fixed biomasses and n-k biomasses to be estimated, ECOPATH solves the simultaneous system of n-k equations which can be expressed as A x B = C, where B is the vector of dimension n-k consisting of only the n-k unknown biomasses, C is the n-k dimensional vector where entry i is the fishery catch of the species group i (with unknown biomass) plus the predation on that species group by all the k species groups with known biomasses. A is the n-k dimensional matrix which determines production, natural mortality and prey-predator relationships within the group of n-k species for which the biomasses are unknown. In other words, when biomasses are fixed the predation from those groups with known biomasses on those groups with unknown biomasses are treated as "catches" and added to the C vector and the rank of the simultaneous system of biomass equations is reduced accordingly. For a species group with known biomass, the only use of that species group in ECOPATH is to determine the predation of that species group on the species groups with unknown biomasses. If both biomasses and catches are entered for the same species group, ECOPATH does not determine if the production and natural mortality of that species group is consistent with the fishing mortality. This is something that could be done and then one of the input parameters for that species group could be estimated.

I would be thankful if Network members let me know if they still have problems after making the code changes in the box below. I am most willing to assist users in their analysis and in the resolution of any problem that may occur.

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Polovina, J.J. and M.D. Ow. 1983. ECOPATH: a user's manual and program listings. Southwest Fish. Cent. Admin. Rep. H82-83 NMFS, Honolulu, 46pp.

Corrections for ECOPATH listings in Polovina and Ow (1983)

- Delete lines 4110,4120,4130 and 4140
- Add the following lines between 4070 and 4080:

```
4071 FOR I = 1 to N
4072 FOR J = 1 to N
4073 AA(I,J) = 0#
4074 IF (I=J) THEN AA(I,J) = 1#
4075 NEXT J
4076 NEXT I
```

- Add the following line between 5270 and 5280:

```
5275 IF (NFLAG(I) = 1 AND
CFLAG(I) = 1) THEN B(I)=
OLBD(I)* HABAR(I)
```

- Correct spelling of "EQUILIBRIUM" on lines 3920,4790,4800 and 5450

8678

Fortunes to be made on the deep slopes

The fishery resources of Pacific islands are often thought, even by people familiar with the Pacific, to consist only of the open ocean species such as tuna and billfish and the near-shore fishes and crustaceans found on shallow coral reefs.

However, on the deep slopes of the islands, there are fishery resources which are heavily exploited in only a few places, such as Hawaii. These resources represent an opportunity to expand island fisheries for small and medium sized multipurpose vessels.

The ex-vessel value of the fisheries for the deep slope resources in Hawaii for 1985 was conservatively estimated to be over $10 million.

The Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service (NMFS) has conducted research on deep slope resources in Hawaii and the Marianas.

One aspect of this work has been to estimate the maximum sustainable yields for a number of the deep slope resources. Many of the same deep slope fish and invertebrates occur throughout the Pacific.

The maximum sustainable fishery yields per area of appropriate habitat appear fairly constant among the Pacific islands. Thus the yields found in Hawaii and the Marianas can be used as first approximations for fishery devlopment in other Pacific islands.

Perhaps the most common to all the islands are the bottom fish — jacks, snappers, and groupers found along the deep slopes at depths from 80 to 300 m. These fish usually weigh from 2 to 10 kg although some of the groupers can weigh over 100 kg.

The South Pacific Commission's outer reef fishing program, together with NMFS survey work, has produced data for over 20 island archipelagoes. These show that most of the same species are found all across the Pacific but that the relative contribution of any species to the group at any island varies considerably.

In Hawaii the bottom fish resource is fished by recreational and commercial fishermen from vessels primarily in the 6 to 15 m range; hook-and-line gear operated with electric or hydraulic gurdies is used.

These fish command a high price. In 1984, the average wholesale price was $5.83/kg, while the two highest priced species averaged $8.80 and $7.37/kg. However, these prices vary considrably with supply.

Based on our research in Hawaii and the Marianas we have found that it is useful to measure the habitat for these fishes as the length of the 100 fathom depth contour. We estimate that a yield of 250 kg of bottom fishes per nautical mile of 100 fm isobath appears to represent a reasonable

Right: A large snapper caught in the Hawaiian Islands. (Photo J. Rutka). Far right: A large grouper caught in the Mariana Islands.

achipelago average for the maximum sustainable yield that can be expected from the bottom fish resource.

Thus an island chain with a length of 100 fm isobath of 500 nmi (about the size of the Marianas) can expect a maximum sustainable yield of 125 metric tons per year from its deep slope bottom fish fishery.

At a price of $5/kg this landing would be valued at $0.6 million. If the resource were fished by a fleet of 20 vessels the average landing per vessel would be 6.3 metric tons valued at $31,250.

Another deep slope resource which appears Pacific wide is deepwater shrimp. These are caught in baited traps in depths from 400 to 750 m. Although these shrimps (there are several related species) command a premium price (about $5.50/kg in Hawaii), the depth at which they are caught makes fishing for them an expensive proposition.

There have been several commercial ventures for these resources both in Hawaii and the Marianas but most have not proven successful. We estimate an archipelago average maximum sustainable yield of 200 kg of shrimp per square nautical mile of habitat.

Thus for an archipelago which has 1000 square nautical miles of habitat in the appropriate depth range (which is about the area of the deepwater shrimp habitat in the Marianas) the annual maximum sustainable yeild for the deepwater shrim resource is 200 metric tons. At a price of $5.50/kg the value of this landing would be $1.1 million.

Again, a fleet of 20 vessels harvesting this resource would have an average annual landing per vessel of 10 metric tons with a value of $55,000.

Although the value of these deep slope resources is very small in comparision to tuna, they are significant compared to the shallow water reef resources. Further they can be fished with small to to medium sized vessels and can be marketed locally on most islands to hotels and restaurants.

The biggest concerns facing development of deep slope fisheries are over capitalisation and overfishing. Initial catch rates in certain areas may be very high and when extrapolated over the habitat area of the archipelago may encourage large capital investment in the fishery.

However, these initial catch rates should not be taken to represent long term averages. Due to the limited habitat area it is easy to heavily fish the deep slope resources; to avoid the boom and bust cycle which often occurs in island fisheries it may be necessary to regulate the fishery. — *Jeffrey Polovina. The author is leader of the Artificial Reef and Enhancement Program at the National Marine Fisheries Service, Honolulu Laboratory.*

8679

A VARIABLE CATCHABILITY VERSION OF THE LESLIE MODEL WITH APPLICATION TO AN INTENSIVE FISHING EXPERIMENT ON A MULTISPECIES STOCK

Jeffrey J. Polovina[1]

ABSTRACT

A variable catchability version of the Leslie model is developed which permits the catchability of one species to vary inversely with the abundance of competing species. This model is used to fit data from an intensive fishing experiment conducted on a multispecies bottom fish stock in the Marianas where catchability of a subordinate species is inversely related to the abundance of a more dominant species. Analysis of this multispecies intensive fishing experiment produced estimates of exploitable bottom fish density in the 150-275 m depth range of 10,156 fish per nmi^2 or 1,354 fish per nmi of 183 m (100-fathom) contour.

Intensive fishing of a closed population can produce data to estimate the initial population size and the catchability coefficient of fish stocks. Two frequently used models applied to intensive fishing data are the Leslie model and the Delury model (Ricker 1975). The Leslie model expresses catch per unit effort (CPUE) at any point during the period of intensive fishing as a linear function of the cumulative catch to that point, whereas the Delury model expresses the logarithm of CPUE at any point during the intensive fishing experiment as a linear function of the cumulative effort. From a statistical viewpoint the Leslie model is often preferable to the Delury model, since a predictive linear regression is used to estimate the parameters of both models and since typically catch is measured more accurately than effort.

Both the Leslie and Delury models assume that catchability is constant during the period of intensive fishing. However, experience indicates that this assumption may not always be satisfied (Pope and Garrod 1975; Schaaf 1975; MacCall 1976; Ulltang 1976; Garrod 1977; Peterman and Steer 1981; Fox[2]). Several authors have found that competition for baits between fish of different size or species can alter catchability (Allen 1963; Rothschild 1967). In this paper a variable catchability Leslie model will be developed for multispecies application where, due to species interactions, the catchability of one species is altered by the presence of other species. This variable catchability Leslie model will be applied to multispecies intensive fishing data from snapper (family Lutjanidae) populations where the application of the constant catchability Leslie model leads to biologically untenable results.

VARIABLE CATCHABILITY LESLIE MODEL

The CPUE during a time interval t (CPUE(t)) is defined as the product of catchability (q) and the mean population size (number of individuals) present during the period t ($N(t)$), thus

$$\mathrm{CPUE}(t) = qN(t). \tag{1}$$

Suppose that up to the beginning of period t, $K(t)$ fish have been caught and removed. If the period t is relatively short, the population of fish closed or isolated, and the fishing pressure heavy enough so that it can be assumed that mortality from other factors is negligible, then $N(t)$ can be expressed as

$$N(t) = N(0) - K(t),$$

where $N(0)$ is the initial population size at the beginning of the experiment ($t = 0$). Inserting this expression for $N(t)$ in Equation (1) produces the Leslie model:

$$\mathrm{CPUE}(t) = q(N(0) - K(t)). \tag{2}$$

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[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

[2] Fox, W. W. 1974. An overview of production modelling. U.S. National Marine Fisheries Service, Southwest Fisheries Center, Administrative Report LJ-74-10, La Jolla, CA.

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Henceforth, this model will be referred to as the constant catchability Leslie model.

In a multispecies situation, competition between species for baited hooks may produce a dominance hierarchy where some species are more aggressive feeders than others and effectively out compete the less aggressive feeders for baited hooks. The catchability of the species at the top of the dominance hierarchy, is independent of the presence of more subordinate species, while the catchability of those species not at the very top of the hierarchy will vary inversely with the abundance of the more dominant species. A simple model which describes the catchability of a subordinate species ($q(s,t)$) as a function of the cumulative catch and initial population size of the more dominant species, $K(d,t)$ and $N(d,0)$ respectively is

$$q(s,t) = q(s)(K(d,t)/N(d,0)) \qquad (3)$$

where $q(s)$ is the catchability of the subordinate species in the absence of the dominant species. Combining Equations (2) and (3) produces

$$\mathrm{CPUE}(s,t) = q(s)(K(d,t)/N(d,0)) \times (N(s,0) - K(s,t)) \qquad (4)$$

and by defining $K(ds,t) = K(d,t)K(s,t)$, $B1 = q(s)(N(s,0)/N(d,0))$, and $B2 = q(s)/N(d,0)$ Equation (3) becomes

$$\mathrm{CPUE}(s,t) = B1K(d,t) - B2K(ds,t).$$

Estimates of $B1$ and $B2$ are obtained from multiple linear regression and the estimates of $N(s,0)$ and $q(s)$ are computed as

$$\hat{N}(s,0) = \hat{B}1/\hat{B}2, \text{ and } \hat{q}(s) = \hat{N}(d,0)\hat{B}2.$$

The estimate of $N(d,0)$ is determined from the constant catchability model. As is evident from Equation (4), the estimate of $N(s,0)$ is independent of the estimate of $N(d,0)$. Estimates of the variance of the estimate of $N(s,0)$ are obtained from estimates of the means and variances of the estimates of $B1$, and $B2$ and an exact expression for the variance of a ratio (Frishman 1975). Thus,

$$V(\hat{N}(s,0)) = V(\hat{B}1/\hat{B}2) = \frac{V(\hat{B}1)[E(\hat{B}2)]^2 - V(\hat{B}2)[E(\hat{B}1)]^2}{(E(\hat{B}2))^2\,[V(\hat{B}2) + [E(\hat{B}2)]^2]} \qquad (5)$$

where $V(\ )$ and $E(\ )$ represent the variances and means, respectively.

APPLICATION OF MULTISPECIES LESLIE MODEL TO SNAPPER INTENSIVE FISHING

A 13-d intensive fishing experiment covering the period 10-19 April and 5-7 May 1984 was conducted at Pathfinder Reef (lat. 16°30′N, long. 143°05′E) in the Mariana Archipelago. Pathfinder Reef is a circular pinnacle rising steeply from a depth of about 1,600 to 16 m beneath the surface. At the 200 m contour, the diameter is about 0.8 nmi (Fig. 1). The snapper population at Pathfinder Reef is a closed population for purposes of the intensive fishing since the closest bank is a small pinnacle 40 nmi to the north.

Intensive fishing was conducted from the NOAA ship *Townsend Cromwell* using four bottom handlines on hydraulic gurdies targeting species in the 150-275 m depth range. Each day during the 13-d experiment, fishing was conducted around the entire perimeter of the bank. During the experiment 1,467 bottom fish were caught. Three lutjanids, *Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus*, accounted for 1,317 fish or about 90% of the catch (Table 1). Fishing effort was measured in

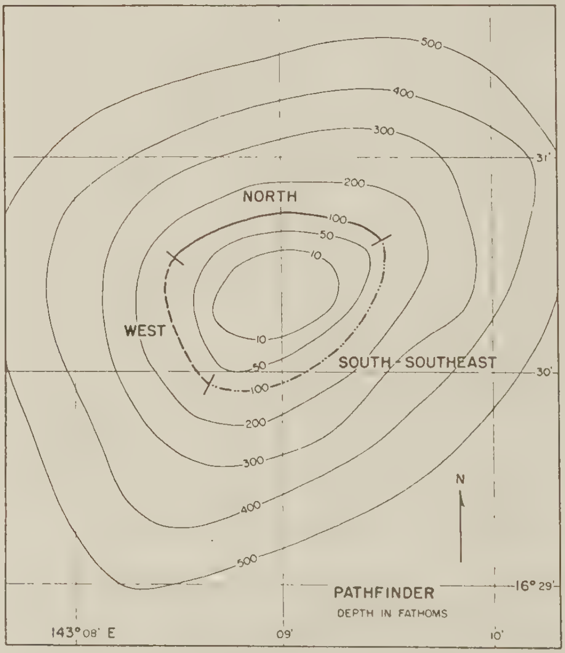

FIGURE 1.—Bathymetric chart of Pathfinder Reef showing the segments of the 100-fathom (183 m) contour used to partition daily fishing effort.

TABLE 1.—Species composition of bottom fish catch at Pathfinder Reef.

Species	Number caught	Percent of catch
Lutjanidae		
Aphareus rutilans	4	0.27
Aprion virescens	1	0.07
Etelis carbunculus	314	21.40
Pristipomoides auricilla	262	17.86
P. filamentosus	16	1.09
P. flavipinnis	7	0.48
P. zonatus	741	50.51
Carangidae		
Caranx lugubris	83	5.66
Seriola sp.	32	2.18
Serranidae		
Cephalopholis igarasiensis	2	0.14
Epinephelus cometae	2	0.14
Saloptia powelli	3	0.20
Total	1,467	100.00

line-hours. As is indicated in Figure 1, the circumference of the reef can be divided into three segments—north, west, and south-southeast, each having similar species composition (Table 2). Further, an attempt was made daily to allocate a consistent proportion of the day's fishing effort to each segment. The proportion allocated to each segment was influenced by the length of each segment and wind and current conditions. On the average, the proportion of the total daily effort allocated to each segment was 0.45 on the south-southeast, 0.21 on the north, and 0.34 on the west. A chi-squared test applied to the daily allocation of fishing effort indicates that there was no significant departure ($P = 0.89$) from this allocation during the course of the fishing experiment. Since the effort was reasonably constant over the duration of the experiment and the entire reef was fished each day, catch, effort, and CPUE computed on a daily basis were used in the analysis. An adjustment to cumulative catch suggested by Chapman (1961) was subsequently shown to improve the model fit in the Delury model (Braaten 1969). This adjustment computes cumulative catch for interval i as the cumulative catch to interval i plus one half the catch during interval i. This adjustment compensates for the decline in CPUE within each time interval. The adjusted cumulative catch is used as the independent variable in all subsequent analyses (Table 3).

TABLE 2.—Species composition for the three segments of the circumference of Pathfinder Reef (see Figure 1).

Species	South-Southeast		North		West	
	No.	%	No.	%	No.	%
Pristipomoides zonatus	358	51	160	68	223	58
P. auricilla	170	24	37	16	55	14
Etelis carbunculus	171	25	39	17	104	27

Plots of CPUE against adjusted cumulative catch for each of the three species of snappers show a decline in CPUE for *P. zonatus*, a slight decline for *E. carbunculus*, and an increase for *P. auricilla* (Fig. 2). A regression line fitted to these data results in negative slopes for *P. zonatus* ($P = 0.0007$) and *E. carbunculus* ($P = 0.05$) and a positive slope for *P. auricilla* ($P = 0.008$). The constant catchability Leslie model fitted the *P. zonatus* data well and resulted in an R^2 of 0.71 and a pattern of residuals which supports the linear model. The estimates of $N(0)$ and q for *P. zonatus* from this fit are 1,066 fish and 0.0038 per line-hour. Due to the selectivity of the fishing gear, $N(0)$ estimated from this intensive fishing data does not represent total population size

TABLE 3.—Daily catch, effort, catch per unit of effort (CPUE), and adjusted cumulative catch for *Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus*

		Total			*Pristipomoides zonatus*			*P. auricilla*			*Etelis carbunculus*		
Date 1984	Effort (line-hours)	Catch (no.)	CPUE	Adjusted cumulative catch	Catch (no.)	CPUE	Adjusted cumulative catch	Catch (no.)	CPUE	Adjusted cumulative catch	Catch (no.)	CPUE	Adjusted cumulative catch
Apr. 10	27.5	152	5.53	76	98	3.56	49	12	0.44	6	42	1.53	21
Apr. 11	23.7	150	6.33	227	111	4.68	153.5	17	0.72	20.5	22	0.93	53
Apr. 12	21.3	100	4.67	352	47	2.21	232.5	12	0.56	35	41	1.93	84.5
Apr. 13	29.7	139	4.68	471.5	91	3.06	301.5	29	0.98	55.5	19	0.64	114.5
Apr. 14	29.3	112	3.82	597.0	66	2.25	380	17	0.58	78.5	29	0.99	138.5
Apr. 15	17.5	84	4.80	695.0	50	2.86	438	13	0.74	93.5	21	1.20	163.5
Apr. 16	30.7	129	4.20	801.5	67	2.18	496.5	26	0.85	113	36	1.17	192.0
Apr. 17	21.4	65	3.04	897.5	38	1.78	548	12	0.56	132	15	0.70	217.5
Apr. 18	22.4	81	3.62	970.5	41	1.83	587.5	15	0.67	145.5	25	1.12	237.5
Apr. 19	21.6	60	2.78	1,041	28	1.30	622.0	17	0.78	161.5	15	0.69	257.5
May 5	20.3	82	4.04	1,112.5	40	1.97	656	29	1.43	184.5	13	0.64	271.5
May 6	22.8	91	3.99	1,199.0	35	1.54	693.5	35	1.54	216.5	21	0.92	288.5
May 7	24.1	72	2.99	1,281	30	1.25	726.0	27	1.12	248.5	15	0.62	306.5

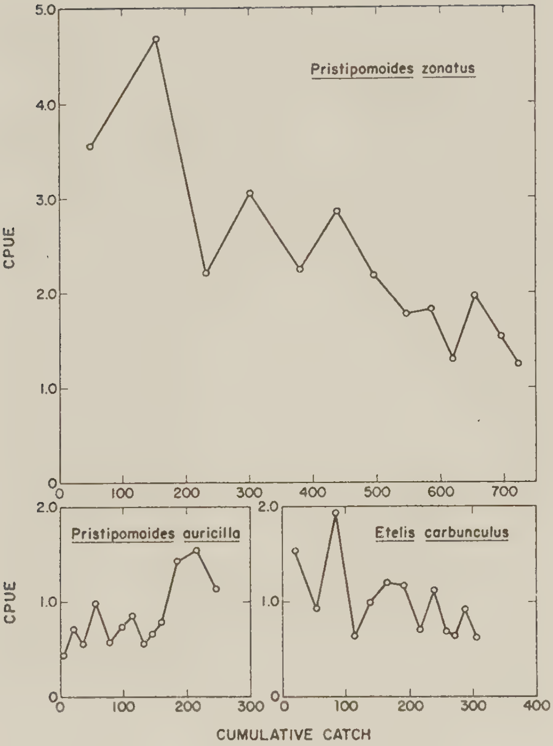

FIGURE 2.—Daily catch per unit effort (CPUE) and adjusted cumulative catch for *Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus*.

but rather the population size of those fish that can be caught by the fishing gear which will be termed the exploitable population. Although the constant catchability Leslie model does not explain as much of the variation for *E. carbunculus* ($R^2 = 0.35$) as it does for *P. zonatus*, the regression is significant and the pattern of residuals supports the linear fit. The estimates for catchability and initial exploitable population size for *E. carbunculus* from the fit of this model are 0.0025 per line-hour and 583 fish. The positive slope for the regression of CPUE on cumulative catch for *P. auricilla* does not make sense biologically under the constant catchability Leslie model.

The depth of capture data show that *P. zonatus* and *P. auricilla* were caught in the same depth range, whereas *E. carbunculus* was typically caught at somewhat greater depths (Table 4). Thus, species interactions would most likely occur between *P. zonatus* and *P. auricilla*. If *P. zonatus* is more aggressive than *P. auricilla* in pursuing fishing baits or in some other way affects the behavior of the latter, then the initial catchability for *P. auricilla* will be low but will rise as the population of *P. zonatus* is reduced. Applying the variable catchability Leslie model to the *P. auricilla* data, with the assumption that *P. zonatus* is the dominant species and that *P. auricilla* is the subordinate species so that the catchability of *P. auricilla* depends on the population size of *P. zonatus*, results in the following relationship:

TABLE 4.—Percent of catch by depth (in fathoms, 1 fathom = 1.83 m).

Species	Depth <100	100-120	>120
Pristipomoides zonatus	15.1	71.7	13.2
P. auricilla	12.6	79.0	8.4
Etelis carbunculus	1.9	46.5	51.6

$$\mathrm{CPUE}(a,t) = q(a)(K(z,t)/N(z,0)) \times (N(a,0) - K(a,t)), \quad (6)$$

where $q(a)$ is the catchability of *P. auricilla* in the absence of *P. zonatus* and $N(z,0)$ and $N(a,0)$ are the initial exploitable population sizes of *P. zonatus* and *P. auricilla*, respectively, and $K(z,t)$ and $K(a,t)$ are the cumulative catch of *P. zonatus* and *P. auricilla* to time t, respectively.

Using the estimate of $N(z,0)$, 1,066 fish, from the fit of the constant catchability model to *P. zonatus* data, Equation (6) has two unknowns to be estimated—$q(a)$ and $N(a,0)$. A multiple linear regression model estimates the initial exploitable population size of *P. auricilla*, $N(a,0)$, at 2,007 fish and $q(a)$ at 0.00087. The variable catchability Leslie model fits the *P. auricilla* CPUE data well and produces an R^2 of 0.89 (Fig. 3). The estimates of initial population sizes for the three species are summarized in Table 5 together with their 95% confidence intervals. For the constant catchability model, the population size confidence interval is computed from a relationship derived by Delury (1958), whereas the confidence interval for the variable catchability model is computed from the variance expression given in Equation (5).

DISCUSSION

The constant catchability Leslie model fit the *P. zonatus* and *E. carbunculus* data well but was not appropriate for the *P. auricilla* data. The variable catchability Leslie model fit the *P. auricilla* data well and provided a plausible explanation for the observed increase in CPUE. Given that there was a time delay between the first 10 d of the intensive fishing (10-19 April) and the last 3 d (5-7 May), and that the greatest increase in the catchability of *P. auricilla* occurred after the time delay, it is possible that the increase in catchability might have a time lag component associated with it. However, given the short time series of data, it would be difficult to test the appropriateness of a more complicated time lag model.

Based on the fit of these two models the initial exploitable population of the three species in the 150-275 m depth range at Pathfinder Reef is estimated at 3,656 fish (Table 5). If we assume, based on the species composition data (Table 1), that these three species represent 90% of the exploitable population then the total exploitable population at the beginning of the intensive fishing is 4,062 fish.

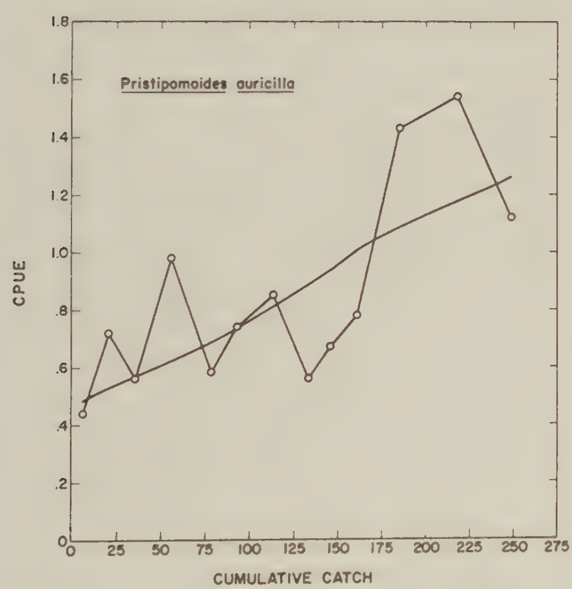

FIGURE 3.—Daily catch per unit effort (CPUE) and predicted CPUE based on the variable Leslie model as a function of adjusted cumulative catch for *Pristipomoides auricilla*.

From Figure 1 the length of the 183 m (100-fathom) contour is estimated at 3.0 nmi, and the area in the 180-300 m depth range is estimated to be 0.4 nmi^2. With these area measures, density estimates of 1,354 fish per nmi of (183 m) 100-fathom contour and 10,156 fish/nmi^2, are obtained for Pathfinder Reef.

Estimates of bottom fish densities based on visual observation from a submersible at Johnston Atoll were 57,281 fish/nmi^2 for the 92-183 m (50-100 fathom) depth range and 66,199 fish/nmi^2 for the 1983-274 m (100-150 fathom) depth range (Ralston et al. 1986). These figures are considerably larger than both the point and interval estimates presented here. Significantly, the study of Ralston et al. (1986) also employed the *Townsend Cromwell*, and the catch rates were comparable at Pathfinder and Johnston (e.g., 3.18 bottom fish/line-hour for the latter). Thus the difference between estimates of standing stock is likely not due to differences in absolute abundance but rather to differences between exploitable population size and total population size. For example, at Johnston Atoll at least 69 species of fish were observed from the submersible, whereas only 10 species were taken by fishing gear in the same depth (Ralston et al. 1986).

If the constant catchability Leslie model is applied to the pooled data for the three species, an estimate of exploitable population size of 2,689 is obtained, about 71% of the estimate of the exploitable population size for the three species when they are estimated separately (Table 5).

Size-specific behavior has been raised as a factor which might affect catchability (Allen 1963). For all three species, there is no evidence of intraspecies size-specific behavior affecting catchability since for two of the species the constant catchability model fits well and for the third species, catchability depends only on the population size of an interacting species. Further, under the hypothesis that within a stock catchability is size-specific across the

TABLE 5.—Estimates of population size and catchability for three species.

Species	Model	R^2	Catch-ability	SE	Initial population size	Confidence interval (95%)
Pristipomoides zonatus	Constant catchability	0.71	0.0038	0.0075	1,066	(803-1,691)
Etelis carbunculus	Constant catchability	0.35	0.0025	0.0010	583	(361-3,011)
P. auricilla	Variable catchability	0.89	0.00087	0.00031	2,007	(261-5,727)
Three species pooled	Constant catchability	0.66	0.0022	0.0047	2,689	(1,955-4,535)

range of exploitable size, intensive fishing would produce a substantial change in the population size structure. A plot of the mean fork length by day of fishing for the three species (Fig. 4) shows very little change in fork length even for *P. zonatus* where 68% of the exploitable stock is estimated to have been removed. Thus, the mean size of the fish in a catch may be a much less sensitive indicator of changes in the population size than catch rates, at least over the short term.

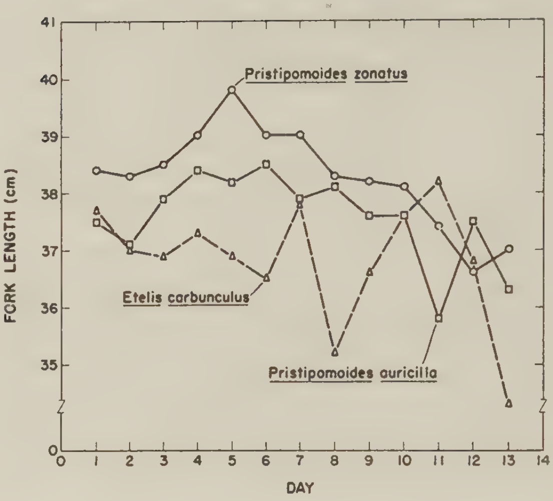

FIGURE 4.—Mean fork length for each day of fishing for *Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus*.

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SOME RESULTS FROM RESEARCH ON JAPANESE ARTIFICIAL REEFS

Jeffrey J. Polovina
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96812 U.S.A.

Over the past 10 years the Japanese have spent US$50 million annually to construct fishing grounds by deploying artificial reefs. Some recent translations of research on the species composition, behavior of fishes, and catches at Japanese artificial reefs are reviewed.

Three studies on different artificial reefs compare the species composition of fishes caught by gill nets and trammel nets at artificial reefs with catches from nearby at flat bottom sites with similar oceanographic conditions (Kakimoto 1979; Kawasaki 1984; Hori 1985). All three studies report that there is a difference in the species composition between the artificial reef and flat bottom sites. In general species including rockfish (Sebastidae), rock trout (Hexagrammidae), scorpionfish (Scorpaenidae), and sea bass (Serranidae) were more abundant at the artificial reefs than on the flat bottom areas. Overall these studies found that when commercially valuable species were considered, the artificial reefs had standing stocks which were 1.5 to 2.5 times higher than the flat bottom areas.

Sakai (1982) compared the catches of three resident demersal species in a 5-year period at a site before the deployment of an artificial reef with the catches from two 5-year periods immediately after the deployment of the artificial reef. The three species groups considered were flatfish, scorpionfish, and octopus. In the first and second 5-year periods after the deployment of the artificial reef the catches of flatfishes had declined to 63 and 67%, respectively, of their level during the 5-year period before the deployment of the reef. The catches of scorpionfish in the first and second 5-year periods after the deployment of the reef increased 18 and 50%, respectively, from their level during the 5-year period before the deployment of the reef. The catches of octopus in the first and second 5-year periods after the deployment of the reef increased 80 and 111%, respectively, from their level during the 5-year period before the deployment of the reef. The total catches of the three species combined in the first and second 5-year periods after the deployment of the artificial reefs increased 13 and 30%, respectively, from their level during the 5-year period before the deployment of the artificial reef. However, Sakai concluded that the increase in catches did not produce a sufficient increase in revenues to justify the cost of the artificial reef when it was amoritized over its 20-year expected life.

Tanaka et al. (n.d.) and Shimizu (1981) used hydroacoustics to examine the distribution of fish schools in an area containing artificial reefs. Both these studies showed that demersal and surface fish schools can at times be found in close proximity to artificial reef sites and that there are also times when there are large schools in the general area but no schools near the artificial reefs.

Studies on catch rates at artificial reef sites nationwide indicate that the annual catch per unit of artificial reef volume ranges from about 0.3 to 12 kg/m^3 (Kakimoto 1985). This range includes large and small artificial reefs and covers a variety of species including migratory demersal and pelagic fishes and a variety of fishing gears. There appears to be a relationship between the enclosed volume of an artificial reef and the annual catch per unit volume from the reef. The maximum catch per unit volume was obtained with reefs of about 3,000 m^3 and the catch per unit volume decreased as the volume of the artificial reef increased or decreased from 3,000 m^3 (Kanamori 1984; Sato and Sakuda 1984).

Even in regions with large artificial reef projects, catches from the artificial reefs do not contribute very greatly to increasing the total catch (Kakimoto 1985). For example, in the Niigata area about 350,000 m^3 of artificial reefs have been installed since 1955 along 250 km of coastline. The average annual landing from that area is about 100,000 metric tons. Even if catches from the artificial reefs averaged 6 kg per m^3, the total catches from the artificial reefs would amount to only 2% of the total landings from the region. However, the artificial reefs do provide valuable fishing grounds for fishermen using small-scale gear targeting high priced fish and it is argued that the benefits offered this sector of the fishing community contribute toward achieving a diverse and stable coastal fishery (Kakimoto 1985).

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AN APPROACH TO YIELD ASSESSMENT FOR UNEXPLOITED RESOURCES WITH APPLICATION TO THE DEEP SLOPE FISHES OF THE MARIANAS

JEFFREY J. POLOVINA AND STEPHEN RALSTON[1]

ABSTRACT

A comprehensive approach to estimate the maximum sustainable yield (MSY) for a tropical multispecies resource which lacks catch and effort data is presented. This yield assessment approach was used to design a fishery resource assessment survey of the Mariana Archipelago. An application of the method is presented to estimate the MSY for a multispecies bottom fish resource, based on data collected during the survey. The annual MSY for the deep slope fishes (primarily snappers and groupers) of the Mariana Archipelago is estimated to be 109 t, which for comparative purposes is equivalent to 222 kg/nmi of 200 m isobath or 0.3 t/km^2.

Assessment of tropical resources has always created major problems in fisheries research (Saila and Roedel 1979; Pauly and Murphy 1982). This has been largely due to three factors: technical difficulties in aging, a high species diversity in tropical communities, and what is typically a multiplicity of artisanal gears used in these fisheries. The latter problem has been especially difficult to surmount, making it difficult to determine not only the level of fishing effort but sometimes even the total catch. Without these data many standard fisheries techniques such as stock-production methods are inapplicable (but see Csirke and Caddy 1983).

In recent years, however, new methods and modifications of existing methods have been proposed to estimate growth and mortality parameters, standing crop, and yield for fish stocks in the absence of a time series of commercial catch and effort data (Beddington and Cooke 1983; Pauly 1983; Polovina 1986a; Wetherall et al. in press). We will show that several of these techniques can be combined, producing an integrated approach to yield assessment designed specifically for tropical fisheries resources in situations where catch and effort data are lacking. The approach is then applied to data gathered in a fishery survey of the Mariana Archipelago to estimate maximum sustainable yield (MSY) for a multispecies resource of deep slope snappers and groupers.

YIELD ASSESSMENT

The equilibrium yield assessment is presented schematically in Figure 1. This approach assumes that growth follows the deterministic von Bertalanffy curve with parameters K and L_∞, that the mortality of fish above the smallest length fully represented in the catch (L_c) occurs at a constant instantaneous rate (Z), and that recruitment is constant with R recruits entering the first vulnerable age class annually. It is also assumed that the resource is essentially pristine, such that an estimate of the biomass recruited to the fishery in the absence of exploitation (B_∞) can be obtained from a catch-per-unit-effort (CPUE) survey and an estimate of catchability. In the discussion section, the effect of relaxing some of these assumptions will be considered.

For each species under consideration, the data required for this program, at a minimum, consist of a large length-frequency sample, otolith data and/or a time series of length-frequency data, a systematic CPUE survey, and an estimate of catchability, such as that obtained from an intensive fishing experiment. The large length-frequency sample is used to jointly estimate the asymptotic length (L_∞) and the ratio of total instantaneous mortality (Z) to the von Bertalanffy growth parameter (K) based on the following relationship:

$$\Theta = Z/K = (L_\infty - \bar{l})/(\bar{l} - L_c),$$

where L_c is a parameter defined above and $\bar{l}$ is the mean length of all fish greater than L_c (Beverton

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[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

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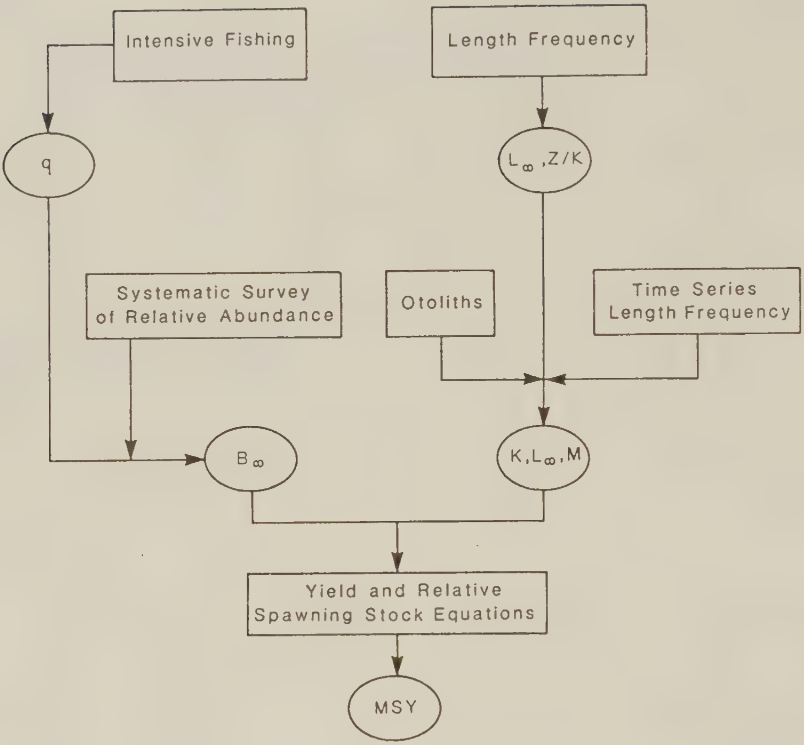
Intensive Fishing
Length Frequency
q
L_∞, Z/K
Systematic Survey of Relative Abundance
Otoliths
Time Series Length Frequency
B_∞
K, L_∞, M
Yield and Relative Spawning Stock Equations
MSY

FIGURE 1.—Schematic of the yield assessment approach. A more general approach to fishery assessment which includes a treatment of catch and effort data as well is given in Munro (1983); our Figure 1 represents a detailed subset of Munro's figure 1 (1983).

and Holt 1956). For a series of L_c values at intervals beginning with the smallest L_c and going up to L_∞, there will be a corresponding set of $\bar{l}$ values. By solving the Z/K equation above for $\bar{l}$ as a function of L_c, the following relationship is obtained:

$$\bar{l} = L_\infty/(\Theta + 1) + L_c\,(\Theta/(\Theta + 1)).$$

Thus, regressing a sequence of $\bar{l}$ values on the corresponding L_c values will produce estimates for the slope and intercept which can be solved for estimates of L_∞ and Z/K (Wetherall et al. in press).

Once an estimate of L_∞ has been obtained by this method, otolith data and/or a time series of length-frequency data can be fit to the von Bertalanffy growth curve to estimate the growth coefficient K. Estimation of L_∞ from length-frequency data was used for the Marianas bottom fish data because a large length-frequency sample was available and otolith readings were difficult to interpret for old stages of growth. With an estimate for K, the total mortality rate, Z, can then be estimated as the product of K and the ratio of Z/K obtained in the previous step. Alternatively, one can estimate Z from a catch curve constructed from a length-frequency sample which has been corrected for nonlinear growth and converted to an age-frequency sample (Pauly 1983).

If these techniques are applied to unexploited or lightly exploited resources, the estimate of Z provides an estimate of the instantaneous rate of natural mortality (M). However, if fishing mortality is believed significant, an equation to estimate M as a function of K, L_∞, and mean annual water temperature (T) (in °C) has been developed as follows (Pauly 1983):

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} \mathrm{T}.$$

Given estimates of K, M, and age of entry to the fishery (t_c), the Beverton and Holt (1957) yield per recruit (Y/R) equation can be used to compute the ratio of equilibrium yield to unexploited recruited biomass as a function of fishing mortality (F). The equilibrium yield (Y) can be expressed as

$$Y = R\,F \int_{t_c}^{\infty} \exp\left(-tM - (t - t_c)\,F\right) w(t)\,dt,$$

where $w(t) = W_\infty\,(1 - \exp(-Kt))^b$, and where W_∞ is the asymptotic weight and b is the exponent of the length-weight relationship. The unexploited recruited biomass (B_∞) can be expressed as

$$B_\infty = R \int_{t_c}^{\infty} w(t)\,\exp(-Mt)\,dt.$$

The ratio of equilibrium yield to unexploited recruited biomass (Y/B_∞) is then independent of W_∞ and R, depending only on K, M, t_c, F, and b. Tables and computational formulae are readily available to evaluate these integrals for Y and B_∞ as functions of t_c and F (Beverton and Holt 1966; Beddington and Cooke 1983). Upon estimation of B_∞, the equilibrium yield is estimated for a given level of F as the product of Y/B_∞ and B_∞.

If a stock is unfished, B_∞ can be estimated by mapping the relative abundance of the stock in terms of CPUE from a systematic survey and then converting estimates of relative abundance into biomass with an estimate of catchability. There are a number of methods which have been used to estimate catchability (Ricker 1975). For work on Pacific island fishery resources, an intensive fishing approach, which fishes a small isolated location heavily and regresses CPUE on cumulative catch (Leslie model), has been used successfully to estimate catchability for bottom fishes and shrimp (Polovina 1986a; Ralston 1986). If only one estimate of catchability is obtained, then the standing stock per unit of area is determined as the ratio of CPUE to catchability in the appropriate units of weight or numbers. If several estimates of catchability are available corresponding to different levels of CPUE, then it might be appropriate to fit a more general power function relationship between CPUE and standing stock (Bannerot and Austin 1983).

The product of Y/B_∞ and B_∞ as a function of F is the equilibrium yield based on the assumption of constant recruitment. While this assumption will be valid for low levels of exploitation, there will come a point as F increases that recruitment will begin to decline and sustainable yield may thus be less than the yield predicted under the assumption of constant recruitment. Estimating MSY yield as the maximum equilibrium yield obtained over all F from the product of Y/B_∞ and B_∞ may, therefore, overestimate the actual MSY. There are two adjustments which have been proposed to estimate MSY in the absence of detailed knowledge of the spawner-recruit relationship. One approach is to estimate MSY from the constant recruitment yield curve as that yield corresponding to that level of F where the addition of one unit of mortality increases the yield by 10% of the amount caught by the first unit of F (Gulland 1983, 1984). This level of mortality and corresponding yield have been denoted as $F_{0.1}$ and $Y_{0.1}$, respectively. A second approach to estimating MSY from the constant recruitment yield curve is to use the Beverton and Holt equation to calculate the ratio of the spawning stock biomass under exploitation (S) to the spawning stock biomass in the absence of exploitation (S_0) and to use this ratio as an indicator of the sustainability of a yield for a given combination of F and t_c. For simplicity, we assume that the age of sexual maturity (t_m) is identical for both sexes. Then the unexploited spawning stock biomass (S_0) is

$$S_0 = R \int_{t_m}^{\infty} \exp(-Mt)\,w(t)\,dt,$$

and

$$S = R \int_{t_m}^{\infty} \exp\left(-Mt - (t-t_c)\,F\right) w(t)\,dt.$$

Thus, the ratio of S/S_0 depends only on M, K, t_c, t_m, and F.

It has been suggested that the spawning stock biomass of a species should not be reduced below 20% of its unexploited level if a substantial reduction in the recruitment is to be avoided (Beddington and Cooke 1983). Thus, the estimate of MSY is determined as the maximum yield from the constant recruitment curve subject to the constraint that F does not exceed the level which reduces the relative spawning stock biomass below 0.20 of S_0.

ASSESSMENT OF SNAPPERS AND GROUPERS IN THE MARIANAS

The Mariana Archipelago consists of a chain of islands and banks on a north-south axis beginning with Galvez Banks and Santa Rosa Reef at the southern end and extending northward to Farallon de Pajaros (30 nmi north of Maug Island). A chain of seamounts also runs on a north-south axis about 120 nmi west of the high island chain (Fig. 2).

Six resource assessment cruises of 40 d each were conducted in the Marianas during the period from May 1982 through June 1984. During these cruises, the deepwater snapper and grouper community along the outer slope was sampled at all 22 islands and banks labeled in Figure 2. Thirteen of these 22 sampling sites were visited at least once during the first three cruises and, again, during the second set

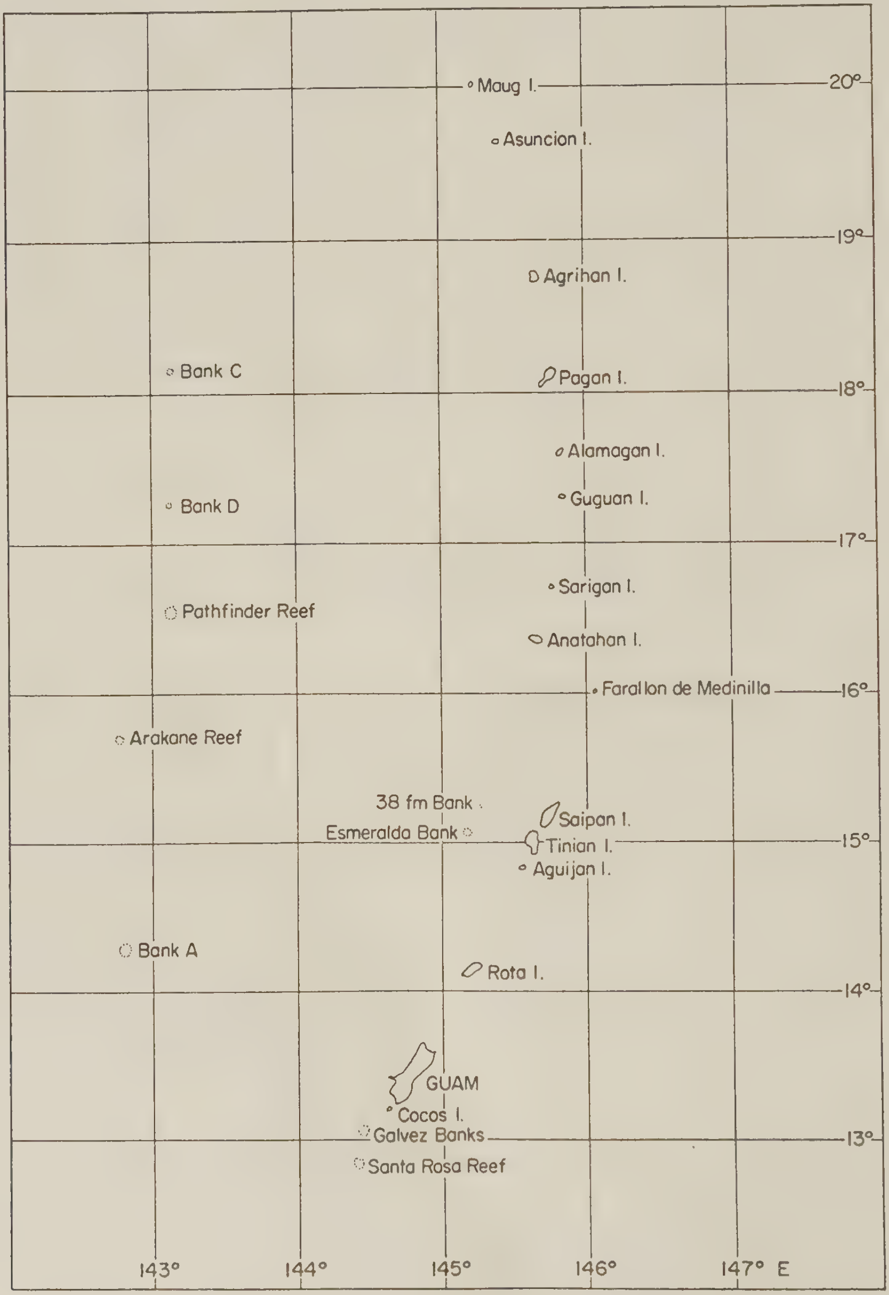
Maug I.
20°
Asuncion I.
19°
Agrihan I.
Bank C
Pagan I.
18°
Alamagan I.
Bank D
Guguan I.
17°
Sarigan I.
Pathfinder Reef
Anatahan I.
Farallon de Medinilla
16°
Arakane Reef
38 fm Bank
Saipan I.
Esmeralda Bank
Tinian I.
15°
Aguijan I.
Bank A
Rota I.
14°
GUAM
Cocos I.
Galvez Banks
13°
Santa Rosa Reef
143°
144°
145°
146°
147° E

FIGURE 2.—The Mariana Archipelago with the 22 islands and banks sampled.

of three cruises. Two sites, Pagan Island and Esmeralda Bank, were sampled on each of the six cruises to establish a time series of length-frequency data.

The NOAA ship *Townsend Cromwell* was used as the fishing vessel for all the cruises. The fishing was conducted from four hydraulic gurdies equipped with 365 m of braided 90 kg Dacron[2] line. The terminal rig consisted of four hooks spaced about 1 m apart and of 2 kg weight.

At each island and bank, an attempt was made to perform a systematic fishing survey of the bottom fish community along the 200 m contour. Fishing was conducted while the vessel drifted and targeted the 125-275 m depth range. Fishing effort was measured in line-hours, defined as the product of the number of lines fished with the length of time, in hours, that they are fished.

Seven species—one jack, *Caranx lugubris*, and six snappers, *Pristipomoides zonatus*, *P. auricilla*, *P. filamentosus*, *P. flavipinnis*, *Etelis carbunculus*, and *E. coruscans*—accounted for about 92% of the catch (Polovina 1986b). Large length-frequency samples were collected for all seven species, primarily from the unfished islands and banks, and were used to jointly estimate M/K, the ratio of instantaneous natural mortality (M) to the growth parameter of the von Bertalanffy growth curve (K), and the asymptotic length (L_∞) by regressing a sequence of mean lengths on minimum lengths (Wetherall et al. in press). Otoliths were collected for all seven species and the growth coefficient K was estimated by fitting a von Bertalanffy growth curve to otolith data with L_∞ fixed at the value estimated from the length-frequency analysis (Ralston and Williams[3]). Once K and the ratio of M/K were estimated, an estimate of M was obtained from their product. The size of entry to the fishery was estimated as the integrated midpoint of the ascending limb of the size-frequency distribution (Gulland 1969). This size was then converted to an age of entry into the fishery (t_c) by application of the von Bertalanffy growth curve. The values of L_∞, K, M, t_m, and t_c for the seven species which are required by the yield analysis are given in Table 1. The exponent of the length-weight equation (b) for most of the species is not significantly different from 3.0, so to simplify the computation, it will be taken as 3.0 for all the species (Ralston in press).

An estimate of the catchability of the bottom fishes which was used to convert CPUE into standing stock was derived from an intensive fishing experiment conducted at Pathfinder Reef (Polovina 1986a). Thirteen days of intensive handline fishing with the *Townsend Cromwell* at Pathfinder Reef produced a substantial and significant decline in CPUE. Application of the Leslie model (Ricker 1975), which regresses CPUE against cumulative catch, produced estimates of catchability for three species—*Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus* (Polovina 1986a). While interesting differences in catchability among species were found, the estimate of the total unexploited biomass for the three species obtained from the species specific Leslie model was not significantly different from the total unexploited biomass computed from the Leslie model applied to the catch and CPUE data pooled over all three species. Catchability from the pooled Leslie model is estimated to be 0.0066 nmi/line-hour. This value was used as an estimate of total

TABLE 1.—Population parameters for the seven major species caught by handlining in the Marianas.

Species	Von Bertalanffy growth parameters L_∞ (cm)	K (1/yr)	Instantaneous natural mortality (M)	Age of entry to the catch t_c (yr)	Age of maturity t_m (yr)
Caranx lugubris	75.1	0.430	0.53	1.3	1.8
Pristipomoides filamentosus	67.3	0.228	0.57	4.3	2.0
P. auricilla	42.6	0.335	0.81	3.6	2.4
P. flavipinnis	54.1	0.238	1.12	3.7	2.2
P. zonatus	47.0	0.245	0.63	4.65	3.25
Etelis coruscans	97.6	0.166	0.38	6.2	4.1
E. carbunculus	69.1	0.175	1.55	3.45	2.75

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3] Ralston, S., and H. A. Williams. Age, growth, and mortality of deep slope lutjanid fishes from the Mariana Archipelago. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396.

bottom fish catchability and was used to estimate standing stock from CPUE.

The systematic survey of relative abundance uses the fishing drift as the basic sampling unit. A drift is defined as the fishing which occurs during an uninterrupted drift by the vessel while fishing continuously in the 125-275 m depth range. The CPUE measured is the number of fish per line-hour and can be computed in two ways for each bank. Bank CPUE will be defined as the total number of fish caught at an island or bank divided by the total number of line-hours fished. Bank mean drift CPUE or simply mean drift CPUE will be defined as the mean of all the individual drift CPUE values for a bank, where the drift CPUE is computed as the number of fish caught within a drift divided by the drift line-hours. While the two measures of CPUE are highly correlated, they are not identical. In our analysis the mean drift CPUE was used as a measure of relative abundance because in a systematic survey the drifts within a bank can be thought of as replicates drawn from the total bank population allowing estimation of within bank variation in CPUE. For a bank, the total standing stock or number of exploitable bottom fishes (N) can be calculated from CPUE, the length (L) of the 200 m contour, and the catchability (q) expressed per nautical mile of 200 m contour as follows:

$$N = (\text{CPUE})\ (L/q).$$

The values of N, CPUE, and L for the banks sampled are given in Table 2.

The catch at any bank can be grouped into eight groups—the seven major species defined previously, plus a group called "others" for all other species. The fraction of the catch (by number) of the total bank catch as determined from fishing surveys, is given in Table 3. The mean weight of each species caught at each site is given in Table 4. For each bank, the unexploited recruited biomass (B_∞) for each of the eight groups is estimated by partitioning the total standing stock into a standing stock for each species group from Tables 2 and 3 and then converting the standing stock for each species group into biomass for each group based on the mean weights in Table 4. Estimates of B_∞ for the eight species groups at each bank are given in Table 5 and the total unexploited biomass is given in Table 6. The estimates of biomass per nautical mile of 200 m contour at Saipan, Tinian, Rota, and Guam are less than half the levels at most other banks. These four islands are the only islands in the Marianas with a substantial resident population. The local fishermen at these islands are known to exploit the bottom fish stocks locally so that estimates of biomass based on bank CPUE values are likely to underestimate unexploited levels. The mean of the biomass per nautical mile of 200 m contour for the two uninhabited islands and one bank in the southern islands is 600 kg. This value was used for unex-

TABLE 2.—Mean drift catch per unit effort (CPUE) and the estimated number of exploitable bottom fish recruited at each bank samples. SE indicates standard error.

Banks and islands	Mean drift CPUE (fish/ line-hour)	SE	Length of 200 m contour (nmi)	Total number of fish at each bank
Maug	5.03	1.02	10.4	7,580
Asuncion	2.16	0.49	11.1	3,480
Agrihan	4.20	0.31	18.3	11,140
Pagan	4.57	0.40	30.0	19,870
Alamagan	2.37	0.19	11.3	3,881
Guguan	3.01	0.30	9.3	4,060
Sarigan	2.82	0.37	8.5	3,470
Anatahan	2.31	0.23	17.2	5,760
Farallon de Medinilla	3.29	0.65	76.9	36,670
Saipan	1.72	0.34	52.6	13,110
38-Fathom	3.12	0.26	2.8	1,270
Tinian	1.96	0.29	28.9	8,210
Aguijan	3.84	0.98	15.9	8,850
Esmeralda	2.29	0.15	12.3	4,080
Rota	1.91	0.40	31.7	8,780
Guam	1.53	0.35	85.2	18,890
Galvez-Santa Rosa	2.95	0.31	52.5	22,450
Bank C	5.91	1.57	3.0	2,570
Bank D	5.85	0.51	3.0	2,540
Pathfinder	4.58	0.23	3.0	1,990
Arakane	3.36	0.24	2.9	1,410
Bank A	3.71	0.57	3.6	1,940

TABLE 3.—The fraction of the number of fish caught at each bank in the eight species groups.

Banks and islands	*Caranx lugubris*	*Pristipomoides filamentosus*	*P. auricilla*	*P. flavipinnis*	*P. zonatus*	*Etelis coruscans*	*E. carbunculus*	Others
Maug	0.016	0.000	0.347	0.016	0.425	0.000	0.102	0.094
Asuncion	0.036	0.036	0.089	0.000	0.589	0.018	0.036	0.196
Agrihan	0.016	0.041	0.103	0.064	0.602	0.016	0.110	0.048
Pagan	0.007	0.002	0.089	0.013	0.699	0.023	0.126	0.042
Alamagan	0.010	0.013	0.232	0.011	0.495	0.143	0.059	0.037
Guguan	0.020	0.004	0.182	0.004	0.613	0.047	0.083	0.047
Sarigan	0.016	0.010	0.141	0.010	0.646	0.042	0.057	0.078
Anatahan	0.015	0.035	0.119	0.148	0.540	0.040	0.045	0.059
38-Fathom	0.064	0.028	0.228	0.047	0.434	0.019	0.045	0.136
Esmeralda	0.017	0.051	0.040	0.366	0.397	0.029	0.026	0.074
Farallon de Medinilla	0.052	0.021	0.093	0.166	0.477	0.021	0.093	0.078
Saipan	0.013	0.138	0.087	0.338	0.225	0.000	0.075	0.125
Tinian	0.000	0.000	0.083	0.694	0.000	0.056	0.139	0.028
Aguijan	0.021	0.188	0.063	0.417	0.271	0.000	0.000	0.042
Rota	0.019	0.143	0.162	0.114	0.362	0.029	0.067	0.105
Guam	0.064	0.161	0.258	0.129	0.161	0.000	0.129	0.097
Galvez-Santa Rosa	0.085	0.017	0.364	0.051	0.322	0.009	0.059	0.093
Bank C	0.000	0.017	0.390	0.000	0.356	0.017	0.212	0.009
Bank D	0.015	0.010	0.091	0.005	0.480	0.045	0.349	0.005
Pathfinder	0.059	0.011	0.172	0.004	0.506	0.000	0.215	0.032
Arakane	0.116	0.057	0.188	0.003	0.412	0.000	0.169	0.055
Bank A	0.008	0.004	0.184	0.008	0.607	0.000	0.159	0.029

TABLE 4.—Mean weight (kg) of the fish caught by bank and species group.

Banks and islands	*Caranx lugubris*	*Pristipomoides filamentosus*	*P. auricilla*	*P. flavipinnis*	*P. zonatus*	*Etelis coruscans*	*E. carbunculus*	Others
Maug	3.784	1.930	0.815	1.585	0.977	6.113	0.893	2.559
Asuncion	3.784	1.930	0.848	1.265	1.344	6.113	0.670	4.595
Agrihan	3.784	1.930	0.784	1.235	1.169	6.113	0.741	7.787
Pagan	3.784	1.930	0.651	1.169	1.094	6.113	0.652	5.068
Alamagan	3.784	1.930	0.834	1.354	1.326	6.113	1.010	2.992
Guguan	3.784	1.930	0.773	1.780	1.216	6.113	0.815	2.400
Sarigan	3.784	1.930	0.642	1.025	1.204	6.113	0.811	5.279
Anatahan	3.784	1.930	0.556	1.169	0.874	6.113	0.586	2.631
38-Fathom	3.784	1.930	0.532	1.193	0.874	6.113	0.798	2.523
Esmeralda	3.784	1.930	0.567	1.014	0.782	6.113	0.702	8.409
Farallon de Medinilla	3.784	1.930	0.439	1.265	0.891	6.113	0.575	1.963
Saipan	3.784	1.930	0.577	0.992	0.837	6.113	0.773	1.353
Tinian	3.784	1.930	0.653	1.003	1.017	6.113	0.422	0.520
Aguijan	3.784	1.930	0.480	0.927	0.760	6.113	0.753	0.770
Rota	3.784	1.930	0.542	1.222	0.667	6.113	0.506	3.168
Guam	3.784	1.930	0.606	1.112	0.780	6.113	0.673	0.600
Galvez-Santa Rosa	3.784	1.930	0.522	1.206	0.979	6.113	0.801	2.085
Bank C	3.784	1.930	0.761	1.265	1.267	6.113	0.923	0.920
Bank D	3.784	1.930	0.961	1.710	1.169	6.113	0.983	1.070
Pathfinder	3.784	1.930	1.953	1.381	1.218	6.113	0.875	7.348
Arakane	3.784	1.930	0.860	1.350	0.949	6.113	0.791	2.338
Bank A	3.784	1.930	0.636	1.605	0.984	6.113	0.811	5.504

TABLE 5.—The unexploited recruited biomass by bank for each species groups in metric tons.

Banks and islands	*Caranx lugubris*	*Pristipomoides filamentosus*	*P. auricilla*	*P. flavipinnis*	*P. zonatus*	*Etelis coruscans*	*E. carbunculus*	*Others*
Maug	0.5	0	2.2	0.2	3.3	0	0.7	1.9
Asuncion	0.5	0.2	0.3	0	2.9	0.4	0.1	3.3
Agrihan	0.7	0.9	0.9	0.9	8.2	1.1	0.9	4.4
Pagan	0.6	0.1	1.2	0.3	15.9	2.9	1.7	4.4
Alamagan	0.1	0.1	0.8	0.1	2.7	3.5	0.2	0.5
Guguan	0.3	<0.1	0.6	<0.1	3.2	1.2	0.3	0.5
Sarigan	0.2	0.1	0.3	<0.1	2.8	0.9	0.2	1.5
Anatahan	0.3	0.4	0.4	1.0	2.8	1.5	0.2	0.9
38-Fathom	0.3	0.1	0.2	0.1	0.5	0.2	<0.1	0.5
Esmeralda	0.3	0.4	0.1	1.6	1.3	0.7	0.1	2.7
Farallon de Medinilla	7.5	1.5	1.6	8.0	16.3	4.9	2.1	5.8
Saipan	0.6	3.6	0.7	4.6	2.6	0	0.8	2.3
Tinian	0	0	0.5	6.0	0	2.9	0.3	0.1
Aguijan	0.7	3.3	0.3	3.6	1.9	0	0	0.3
Rota	0.7	2.6	0.8	1.3	2.2	1.6	0.5	3.1
Guam	4.8	6.1	3.1	2.8	2.5	0	1.7	1.1
Galvez-Santa Rosa	7.5	0.8	4.5	1.4	7.4	1.2	1.1	4.6
Bank C	0	0.1	0.8	0	1.2	0.3	0.5	<0.1
Bank D	0.2	0.1	0.2	<0.1	1.5	0.7	0.9	<0.1
Pathfinder	0.5	<0.1	0.4	<0.1	0.3	0	0.4	0.5
Arakane	0.6	0.2	0.2	<0.1	0.6	0	0.2	0.2
Bank A	0.1	<0.1	0.2	<0.1	1.2	0	0.3	0.3
Total	32.5	32.0	24.5	43.1	85.4	26.2	15.9	42.8

TABLE 6.—The total unexploited recruited biomass (B_∞) in metric tons (t) and the total unexploited recruited biomass per nautical mile (nmi) of 200-m contour in kilograms (kg) by bank.

Banks and islands	Total unexploited recruited biomass (t)	Biomass per nmi of 200 m contour (kg)
Northern banks and islands		
Maug	8.8	850.3
Asuncion	7.7	689.7
Agrihan	18.1	991.1
Pagan	27.0	900.7
Alamagan	8.0	706.8
Guguan	6.1	659.7
Sarigan	6.1	714.0
Anatahan	7.6	440.6
38-Fathom	1.8	637.1
Esmeralda	7.2	584.1
	Total 98.4	Mean 717.4
Southern banks and islands		
Farallon de Medinilla	47.7	620.2
Saipan	15.3	290.9
Tinian	10.0	346.0
Aguijan	10.1	637.0
Rota	12.4	391.2
Guam	22.2	260.6
Galvez-Santa Rosa	28.5	542.4
	Total 146.2	Mean 441.2
Western seamounts		
Bank C	2.9	973.0
Bank D	3.6	1,207.0
Pathfinder	3.1	1,024.0
Arakane	2.0	695.9
Bank A	2.1	594.7
	Total 13.7	Mean 898.9

ploited biomass per nautical mile of 200 m contour in the subsequent yield estimation, in place of the values computed from the bank CPUE values for the inhabited southern islands (Saipan, Tinian, Rota, and Guam).

For each species group with values of K, M, t_c, and F, the ratio of fishery yield to unexploited recruited biomass (Y/B_∞) can be computed from the Beverton and Holt yield equations (Beddington and Cooke 1983). The product of Y/B_∞ with the species group unexploited recruited biomass estimates (Table 5) results in estimates of equilibrium yield for the seven species for which estimates of K and M are available. For the eighth group, which consists of all other species, the ratio of yield to B_∞ is taken as the ratio of total yield for the seven species divided by their total B_∞. For a fixed F, the sum of the equilibrium yield of the eight species groups at a bank is the bank equilibrium yield, and the sum of the equilibrium yields for a species group over all the banks is the species group equilibrium yield.

The equilibrium yield for the multispecies bottom fish complex fished with handline gear in the 125-275 m depth range for the 22 islands and banks of the Mariana Archipelago increases rapidly as a function of F to a level of about 90 t and beyond that exhibits a gradual increase with increased fishing mortality (Table 7). The MSY estimation approach estimates MSY as the yield from the constant recruitment yield curve corresponding to that level of mortality where a marginal increase in one unit of mortality increases the catch by 0.1 of the amount caught by the first unit of F. The value of $F_{0.1}$ for the bottom fish resource in the Marianas is estimated to be $F = 1.0$ and the corresponding annual equilibrium yield is 82 t (Table 7).

TABLE 7.—Total annual sustainable handline yield in metric tons (t) for a range of fishing mortalities.

Fishing mortality (F)	Total yield (t)
0.1	23
0.5	64
[1]1.0	[1]82
1.5	89
2.0	92
2.5	94

[1] $F_{0.1}$ and $Y_{0.1}$ as defined by Gulland (1983).

The equilibrium yield value of 82 t, which corresponds to a fishing mortality of 1.0, is based on the current estimated age of entry to the fishery and not necessarily the age of entry which maximizes the Y/R. For a fishery mortality of 1.0, the estimated age of entry which maximizes Y/R is computed from the Beverton and Holt equation and compared with the current age of entry for each species (Table 8). With the exception of the jack, *Caranx lugubris*, the age of entry which maximized Y/R is less than the current age of entry (Table 8). Based on the age of entry which maximized the Y/R, new levels of sustainable yield for each species group as a function of F can be computed as the product of the yield for the current age of entry with the ratio of Y/R maximized over age of entry to the Y/R for the current age of entry. The values of $F_{0.1}$ and $Y_{0.1}$ for the ages of entry which maximize the Y/R are 1.0 and 109 t, respectively (Table 9). An approximate confidence interval (C.I.) for this yield estimate can be obtained from a Taylor series expansion which incorporates the variance estimate for catchability (Polovina 1986a) and a sampling variance of the bank CPUE values (Table 2). The standard error of the yield estimate is 14 t, and thus a 95% C.I. for the yield at $F_{0.1}$ for the archipelago is 81-137 t annually.

The estimation of MSY based on the relative spawning stock approach requires estimates of the age of sexual maturity (t_m). A relationship expressing the length at sexual maturity (L_m) as a fraction of the length of the upper one percentile ($L_{\max}$) for tropical bottom fishes is as follows (Anonymous 1977, from Brouard and Grandperrin 1984):

$$L_m = 0.576\ L_{\max}.$$

TABLE 8.—Current age at entry and age at entry which maximizes the yield per recruit (Y/R) at $F = 1.0$.

Species	Current age at entry t_c (yr)	Age at entry which maximizes Y/R (yr)
Caranx lugubris	1.3	1.75
Pristipomoides filamentosus	4.3	2.75
P. auricilla	3.6	2.25
P. flavipinnis	3.7	2.00
P. zonatus	4.65	3.00
Etelis coruscans	6.2	4.50
E. carbunculus	3.45	2.50

TABLE 9.—Annual sustainable handline yield in metric tons (t) for the age at entry which maximizes the yield per recruit for each species.

Fishing mortality (F)	Total yield (t)
0.1	35
0.5	91
[1]1.0	[1]109
1.5	114
2.0	116
2.5	116

[1] $F_{0.1}$ and $Y_{0.1}$ as defined by Gulland (1983).

The t_m can then be computed from L_m with the von Bertalanffy growth equation. The t_m for the seven species, which is assumed to be the same for both sexes of a species, is given in Table 1, and the ratio of spawning stock biomass under exploitation to the unexploited spawning stock biomass is presented for three levels of F (Table 10). As expected, the ratio decreases as F increases. However, without the spawner-recruit relationship, it is difficult to determine the extent that the spawning stock biomass can be reduced before recruitment is substantially affected. It has been suggested that as a lower bound, the spawning stock biomass should not be reduced below 20% of its unexploited level before there is a deleterious reduction in recruitment (Beddington and Cooke 1983). The level of $F = 1.0$ is the largest level of F which insures that the relative spawning stock biomass for all the species does not fall below 20% and hence the spawning stock approach also estimates the MSY for the bottom fish in the Marianas at 109 t/year.

TABLE 10.—The ratio of spawning stock biomass to unexploited spawning stock biomass for three levels of fishing mortality (F) at the age of entry which maximizes the yield per recruit.

Species	$F = 0.5$	$F = 1.0$	$F = 2.0$
Caranx lugubris	0.44	0.26	0.12
Pristipomoides filamentosus	0.46	0.33	0.25
P. auricilla	0.45	0.29	0.19
P. flavipinnis	0.45	0.26	0.12
P. zonatus	0.39	0.24	0.14
Etelis coruscans	0.31	0.20	0.13
E. carbunculus	0.58	0.42	0.30

DISCUSSION

The assessment proposed here is a multispecies approach which is most suitable for resources where prey-predator interactions are negligible. Two assumptions initially required to implement this program, i.e., constant recruitment and that the resource be essentially unexploited, can in some instances be relaxed. Simulation results suggest that if recruitment is seasonal and a pooled length frequency is constructed from individual length-frequency samples collected over the year, the length-frequency based method used here to estimate mortality produces an essentially unbiased estimate (Ralston[4]). Furthermore, the assumption that stocks be unexploited can be relaxed if an estimate of the average of F for the archipelago can be obtained. Then M can be estimated by the difference between F and total mortality, and instead of estimating unexploited recruited biomass from the CPUE survey, the biomass under F will be estimated, and yields calculated as the product of exploited biomass with the ratio of yield/biomass resulting from F computed from the Beverton and Holt yield equation.

The estimate of maximum equilibrium yield from the Beverton and Holt (1957) equation for the deep slope snappers and groupers from 22 banks in the Mariana Archipelago is 109 t annually with a fishing mortality of 1.0. About 70% of this yield would be expected to come from the southern islands of the chain, including Guam and Saipan. Another 27% would come from the northern islands and only 3% from the seamounts (Table 11).

The mean of the annual sustainable yield levels per nautical mile of 200 m contour for the northern banks, southern banks, and western seamounts are 212.9, 228.5, and 264.4 kg, respectively, with a ratio of total yield for the archipelago to the total length of the 200 m contour of 222.4 kg/nmi (95%) C.I. of 165.3-279.6) (Table 11). Detailed bathymetry data to establish a correspondence between contour length and area are available from Guguan Island in the northern Marianas, and it is estimated that 1 nmi of 200 m isobath corresponds to 0.23 nmi^2 of habitat in the 125-275 m depth range (Polovina and Roush[5]). Based on this correspondence the unit MSY of 222.4 kg/nmi of 200 m contour for the Marianas is equivalent to about 1.0 t/nmi^2 or 0.3 t/km^2.

These values suggest that the Marianas may be slightly less productive for bottom fishes than the Hawaiian Archipelago where a lower bound estimate for MSY of 272 kg/nmi of 200 m contour was obtained from a stock production model applied to commercial catch and effort data that did not include the recreational fishing component of snappers and groupers. Also, an estimate of 286 kg/nmi of 200 m contour was derived from an ecosystem model applied to an island system in the Northwestern Hawaiian Islands (Ralston and Polovina 1982; Polovina 1984).

The species composition of the catch should depend to some extent on levels of F and t_c. As F increases and t_c decreases, the contribution of

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[4] Ralston, S. The effect of pooling length-frequency distributions on mortality estimation in seasonally breeding fish populations: A Monte Carlo simulation. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396.

[5] Polovina, J. J., and R. C. Roush. 1982. Chartlets of selected fishing banks and pinnacles in the Mariana Archipelago. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. H-82-19, 7 p.

TABLE 11.—Annual sustainable yield in metric tons (t) and yield in kilograms (kg) per nautical mile (nmi) of 200 m contour for the age at entry which maximizes the yield per recruit at a level of fishery mortality of $F = 1.0$.

Banks and islands		Total yield (t/yr)		Yield (kg per nmi of 200 m contour/yr
Northern banks and islands				
Maug		2.7		262
Asuncion		2.1		188
Agrihan		5.6		304
Pagan		7.7		255
Alamagan		2.0		178
Guguan		1.7		179
Sarigan		1.6		194
Anatahan		2.5		144
38-Fathom		0.5		187
Esmeralda		2.9		237
	Total	29.3	Mean	213
Southern banks and islands				
Farallon de Medinilla		16.7		217
Saipan		13.4		254
Tinian		8.8		304
Aguijan		4.2		267
Rota		6.1		192
Guam		17.2		202
Galvez-Santa Rosa		8.6		164
	Total	76.0	Mean	229
Western seamounts				
Bank C		0.9		288
Bank D		1.1		351
Pathfinder		0.9		304
Arakane		0.6		200
Bank A		0.6		180
	Total	4.1	Mean	264

Total yield from all banks: 109 t/yr.
Total yield/length of 200 m contour = 222.3 kg/nmi.

those species to the catch with the high M/K values, particularly *P. flavipinnis* and *E. carbunculus* tends to increase (Table 12). A form of succession is, therefore, predicted as exploitation proceeds.

There are two approximations which have been used to determine MSY which express it as a fraction of the unexploited biomass. Gulland's formula estimates MSY as 0.5 MB, where M is the instantaneous rate of natural mortality and B is the unexploited biomass. An approach proposed by Pauly estimates MSY as $B\,2.3w^{-0.23}$, where w is the mean of the weight (in grams) at sexual maturity and the asymptotic weight (Gulland 1983; Pauly 1983). A comparison of these two estimators with the values obtained here shows that for four out of seven species the Y/B values estimated with the Beverton and Holt equation lie between the values obtained from the Pauly and Gulland approximations.

TABLE 12.—The percentage of annual sustainable yield by species groups for two ages at entry with two levels of fishing mortality.

	Percentage of total catch by weight			
	Current age of entry		Age at entry which maximizes yield per recruit	
Species groups	$F = 0.10$	$F = 1.50$	$F = 0.10$	$F = 1.0$
Caranx lugubris	10.0	5.5	7.3	8.3
Pristipomoides filamentosus	10.3	8.5	9.4	8.2
P. auricilla	8.5	9.4	7.4	7.3
P. flavipinnis	15.6	21.7	24.3	28.7
P. zonatus	28.1	26.7	26.1	23.1
Etelis coruscans	7.6	5.1	7.1	5.0
E. carbunculus	5.9	9.2	4.6	5.9
Others	14.0	13.8	13.8	13.5

For the other three species, the Y/B values fall slightly below the Pauly and Gulland approximations for two species and substantially above for the third species. The mean Y/B values obtained by the Pauly and Gulland approximations are, moreover, in substantial agreement with the mean value of Y/B obtained with the approach proposed here (Table 13).

TABLE 13.—Annual maximum sustainable yield as a fraction of unexploited recruited biomass (Y/B_∞) at F = 1.0 together with 0.5 M and 2.3 $w^{-0.26}$.

Species groups	Y/B_∞	0.5 M	2.3 $w^{-0.26}$
Caranx lugubris	0.261	0.335	0.252
Pristipomoides filamentosus	0.262	0.270	0.296
P. auricilla	0.306	0.325	0.403
P. flavipinnis	0.680	0.475	0.348
P. zonatus	0.280	0.270	0.363
Etelis coruscans	0.201	0.175	0.226
E. carbunculus	0.375	0.515	0.289
Mean	0.338	0.338	0.311

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A MODEL OF THE DRIFT OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE IN THE CALIFORNIA CURRENT

JAMES H. POWER[1]

ABSTRACT

The drift of northern anchovy, *Engraulis mordax*, larvae in the California Current to unfavorable offshore areas may be an important factor contributing to larval mortality, and hence it may affect recruitment and subsequent adult population size. A simulation model based on a finite-difference approximation to the advection-diffusion equation was developed to aid in the study of larval anchovy drift. Model components included the long-term mean geostrophic and wind-driven current velocities to 50 m depth, and turbulent diffusion. The model predicted larval distributions in the Southern California Bight and offshore regions after 30 days of drift, and these distributions were used to assess the extent of cross-shore and alongshore larval transport that occurs when spawning takes place at different locations, seasons, and during times of increased offshore-directed Ekman transport.

Offshore transport was minimal in most simulations. Simulations of drift starting from the location of peak spawning showed strongest seasonal effects, with currents during the season of peak northern anchovy spawning (March) resulting in reduced offshore dispersal when compared with currents at other times of the year. March currents also produced the greatest downshore (southeasterly) transport of larvae, and strong seasonal currents, such as the nearshore, northwesterly flowing California Countercurrent, can greatly affect the alongshore 30-day larval distributions. Offshore directed Ekman transport, associated with upwelling, does not strongly affect the drift of larvae in the nearshore region, but large increases in overall Ekman transport, or extension of spawning into offshore regions, can result in significant seaward transport of larvae out of the Southern California Bight.

The total population of northern anchovy, *Engraulis mordax*, a common pelagic fish off the west coast of North America, is comprised of three subpopulations (Vrooman et al. 1981): northern (found north of lat. 36°30′N); central (between lat. 29° and 38°N); and southern (south of lat. 29°N). The central subpopulation inhabits the Southern California Bight region, and in recent times has exhibited substantial changes in population biomass (e.g., Smith 1972). Analysis of northern anchovy scales deposited in sediments indicates that large northern anchovy population fluctuations have also occurred in the past few centuries (Soutar and Isaacs 1974). Historically the central subpopulation of northern anchovy has supported a significant fishery (Messersmith and Associates 1969; Sunada 1975; Stauffer and Charter 1982), and although the U.S. fishery has recently declined, there is still a significant Mexican fishery. The northern anchovy fishery, the recent and historical changes in anchovy population size, and the fish's important role in the marine ecosystem all provide the motivation for studying the mechanisms that may cause interannual variations in northern anchovy stock size.

Such changes in stock size may be a consequence of variations in the previous spawning stock size, or they can also arise as a result of interannual differences in mortality during prerecruit life history stages (Rothschild et al. 1982). Because the egg and larval stages have the highest mortalities, it seems possible that processes affecting the relative mortality during these stages can have a significant effect on subsequent recruitment. Two major causes of larval mortality are starvation and predation (Smith and Lasker 1978; Hunter 1981). A factor that may contribute to these is larval drift. The northern anchovy eggs and larvae, lacking adequate motility, can be involuntarily transported away from nearshore spawning areas. It is the nearshore regions in the Southern California Bight that most frequently contain adequate food concentrations for growth and survival of first feeding northern anchovy larvae (Lasker 1978, 1981).

Although eddies and other short-term mesoscale features are important in the Southern California Bight (Mooers and Robinson 1984; Simpson et al. 1984), the broad and relatively slow equatorward flow termed the California Current is the dominant feature in the region that persists on evolutionary

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038; present address: Coastal Fisheries Institute, Center for Wetland Resources, Louisiana State University, Baton Rouge, LA 70803-7503.

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time scales. Hence, it seems plausible that northern anchovy spawning strategies have developed in response to the relatively predictable seasonal and spatial trends in the California Current. Possible relationships between time and location of fish spawning and the currents off the west coast of North America have been discussed by Parrish et al. (1981). They noted that in the Southern California Bight the Ekman (wind-driven) currents are generally diminished relative to other areas along the coast. This reduced offshore transport is favorable for the retention of fish eggs and larvae. However, some weak offshore directed Ekman transport is consistently present in the Southern California Bight year round (Nelson 1977; Parrish et al. 1981; Bakun and Parrish 1982).

Smith (1972) analyzed historical records of northern anchovy larval distribution in the Southern California Bight and found that samples taken farther offshore had a higher proportion of older larvae than that of samples taken nearshore. Assuming a uniform spatial and temporal distribution of spawning, this result implied that a significant fraction of northern anchovy eggs and larvae were transported offshore after nearshore spawning. Bailey (1981) found that the average distance offshore of Pacific hake, *Merluccius productus*, larvae north of Point Conception was positively correlated with offshore Ekman transport and that the magnitude of subsequent Pacific hake recruitment was negatively correlated with offshore transport. Hewitt and Methot (1982) compared the distributions of northern anchovy larvae sampled in 1978 and 1979 and found that the bulk of the larvae in 1979 were farther offshore than those in 1978 and that mortality of 0-group northern anchovy was greater in 1979 when compared with those spawned in 1978. The year 1979 was one of enhanced upwelling and colder temperatures (both concomitants of offshore Ekman transport) relative to 1978.

The studies cited above suggest drift may play an important role in larval ecology, but the conclusions drawn from plankton sampling must be viewed with caution. Inferences drawn from field collections about the drift of larvae usually carry the assumption that both northern anchovy spawning and larval mortality were uniform in space and time, because the time and distance scales involved largely preclude synoptic sampling of eggs and larvae throughout the region. Hence, only correlative explanations for the observed distribution can be made, and other causal factors affecting the larval distribution may be hidden. For example, an observation of greater proportions of older larvae in offshore waters could also result from earlier spawning or greater early mortality (possibly coupled with increased spawning activity) in those waters, and not drift. Additionally, the mesoscale variability present in the Southern California Bight and the considerable patchiness of early and late larvae (due to northern anchovy schooling behavior; Hewitt 1980, 1981a) further confound the conclusions drawn from plankton samples and diminish the value of interannual comparisons. Therefore, as an alternative to field studies, a simulation model of northern anchovy drift in the California Current was developed to help evaluate the role of drift in larval ecology. The objective was to use the model to determine the effect of differences in northern anchovy spawning location and time on the subsequent larval distribution and to evaluate the effects on larval distribution when offshore Ekman transport is increased above its normal mean value.

METHODS

The drift simulation was based on the two-dimensional (x,y) form of the advection-diffusion equation:

$$\frac{\partial F}{\partial t} + \frac{\partial}{\partial x}\left(uF - K_x \frac{\partial F}{\partial x}\right) + \frac{\partial}{\partial y}\left(vF - K_y \frac{\partial F}{\partial y}\right) = 0$$

where F = the concentration of eggs and larvae;
u and v = current velocities in the respective x and y directions; and
K_x and K_y = eddy diffusivity coefficients for the x and y directions.

An analytical solution to this equation cannot be evaluated relative to northern anchovy larval drift in the California Current, although a numerical approximation that specifies larval concentration as a function of location and time can be determined. This was accomplished by approximating each of the derivatives in the equation by weighted finite-differences, so that the model was algebraically formulated as the current and diffusivity-mediated fluxes of larvae among geographic points in the Southern California Bight. Apart from the assumption that larvae continually maintained themselves in surface waters, the northern anchovy were assumed to be conservative and completely passive drifters, i.e., no mortality or movement due to larval swimming was incorporated into the model. Details of the numerical methods used are presented in Power (1984).

The geographic grid for the model was defined using the California Cooperative Oceanic Fisheries Investigation (CalCOFI) coordinate system. The CalCOFI grid is a regular coordinate system of cross-shore "lines" and alongshore "stations". The model and CalCOFI grids are oriented with respect to the coast so that increasing station number corresponds to increasing offshore distance and increasing line number implies the downshore (southeasterly) direction. Each line unit increment is spaced 12 nm apart, and each station unit represents 4 nm. The grid for the model was defined to form cells that were 37 km (20 nm) on a side, and the fluxes of larvae were among grid cell centers. Model coverage was from CalCOFI lines 70 to 120, and extended offshore to CalCOFI station 120 (Fig. 1).

Unless northern anchovy utilize a strategy whereby spawning is initiated in response to the presence of an eddy or other short-term mesoscale features, it can reasonably be expected that spawning time and location have evolved partially in response to predictable current features. For this reason, seasonal currents based on interannual means were used in the model. Northern anchovy spawning behavior relative to eddies, etc., is presently unknown, and there are persistent seasonal trends in spawning, e.g., northern anchovy spawn throughout the year, but March is typically the peak time of spawning (Smith 1972; Methot 1981).

Geostrophic currents for the model were calculated using the geopotential anomalies computed by Lynn et al. (1982). Lynn et al. used CalCOFI data collected between 1950 and 1978 to compute the average geopotential anomaly relative to 500 m for four seasonal periods (nominally January, April, July, and October) at 175 locations in the California Current. Average geopotential anomalies were computed for an additional 23 locations for this study to augment the Lynn et al. (1982) coverage

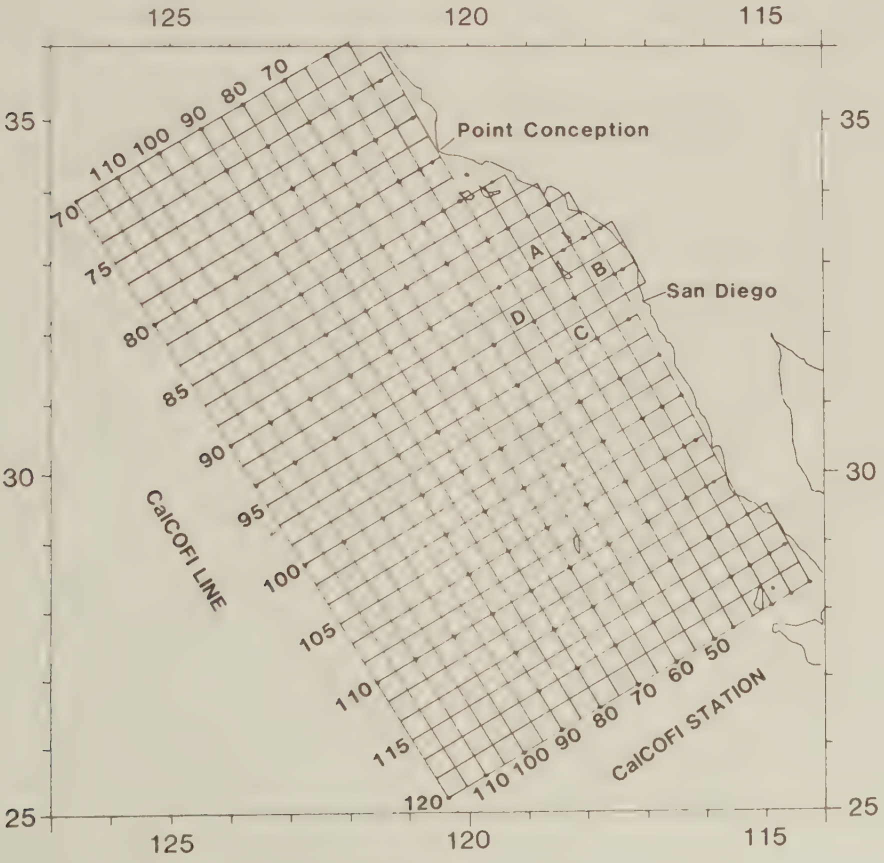


FIGURE 1.—Geographic grid used in the northern anchovy drift simulations, and the corresponding CalCOFI line and station coordinate system. Lettered locations are starting points for simulation presented in this paper. Mean geopotential anomolies (used for computing geostrophic currents) were calculated for the locations indicated by dots (Lynn et al. 1982; this study).

(Fig. 1). The top 50 m of the water column is the predominant depth range of anchovy larvae (Ahlstrom 1959), therefore mean anomaly values for the surface and for 10, 20, 30, and 50 m of depth were used in this study. The anomalies at each standard depth were interpolated to model grid nodes using the bivariate interpolation algorithm of Akima (1978). Geostrophic current velocities normal to each grid cell interface were computed for each of the standard depths, and average geostrophic current velocities were then calculated for a layer extending from the surface to 50 m.

Wind speed and direction data used in this study were from the data base summarized and discussed by Nelson (1977). The raw wind observations were converted to surface wind stress (τ) values using the relation

$$\tau = \rho C_d W^2$$

where ρ = air density (1.22 kg m^{-3});
C_d = drag coefficient; and
W = wind speed.

The drag coefficient was computed as a function of wind speed using the empirical relation of Amorocho and DeVries (1980, 1981). The computed wind stress vectors were partitioned by month of observation and resolved into alongshore and cross-shore components. A monthly mean wind stress component for each model grid cell interface was then computed by averaging the appropriate component of the stress vectors in the 37 km by 37 km area bisected by the grid cell interface. Total Ekman or wind-driven transport in the direction 90° to the right of the wind can be approximated by dividing the wind stress by the Coriolis parameter (Neumann and Pierson 1965), and this calculation was performed for the mean wind stress components. The mixed layer depth in the California Current is seldom >50 m, and is often <20 m in the Southern California Bight during the summer (Husby and Nelson 1982). It was assumed that Ekman transport occurring deeper than 50 m was negligible, and the Ekman transport values were converted to a mean wind-driven velocity for the surface to 50 m layer by dividing the transport by the 50 m layer thickness.

The final current velocities were calculated as the vector sum of the seasonal geostrophic and appropriate monthly Ekman components. Vector addition of the two components appears to be a reasonable assumption (Parrish et al. 1981), and no compensation for redistribution of mass owing to sustained winds was performed. The final seasonal current fields for the simulations were January, March (April geostrophic velocities plus March Ekman velocities), July, and October currents.

Figure 2 illustrates the general trends in the California Current for the January and March seasons. This figure should be interpreted with caution. Apart from the large potential differences between actual synoptic conditions and the average pattern used in the simulations, the resultant vector for a cell was necessarily computed for Figure 2 by averaging the current components of opposing cell faces and then calculating the resultant. A distortion is introduced wherever components on opposite faces of a cell differ in magnitude or sign, so that Figure 2 best represents features of the California Current that are consistent over several model grid cells. The California Current is evident as two regions of intensified southeasterly flow at the left margins and midlines of the plots. During all parts of the year except spring, the current turns toward shore at the southern end of the Southern California Bight. A northwesterly flow near the coast subsequently forms the inshore portion of a large cyclonic eddy (the Southern California Eddy; Owen 1980) that occupies most of the Southern California Bight. During most of the year part of this eddy's northeasterly flow continues past Point Conception, to form the California Countercurrent (Hickey 1979; Fig. 2, January plot). In the spring the southeasterly flow of the California Current moves closer to shore to obliterate the surface portion of the Countercurrent (Fig. 2, March). Tsuchiya (1980, fig. 2) gives a clear picture of the seasonal inshore-offshore movements of the California Current at CalCOFI lines 90 and 93. Close to shore in the southern half of the modeled region there is another region of intensified southeasterly flow, most evident in the March current plot. Lynn et al. (1981) provided detailed illustrations of the geostrophic flow regimes used in the simulations, and Nelson (1977) presented graphical representations of the wind stress fields along the west coast of North America. Hickey (1979) presented a comprehensive review of seasonal and spatial variations of the California Current and the possible driving mechanisms involved, and Owen (1980) reviewed the incidence and ecological consequences of eddies in the California Current system.

Two additional current fields were calculated in order to assess the effects of increased offshore directed Ekman transport on larval northern anchovy distribution. As mentioned earlier, the mean wind stress is consistently directed downshore during March in the modeled region, a condition

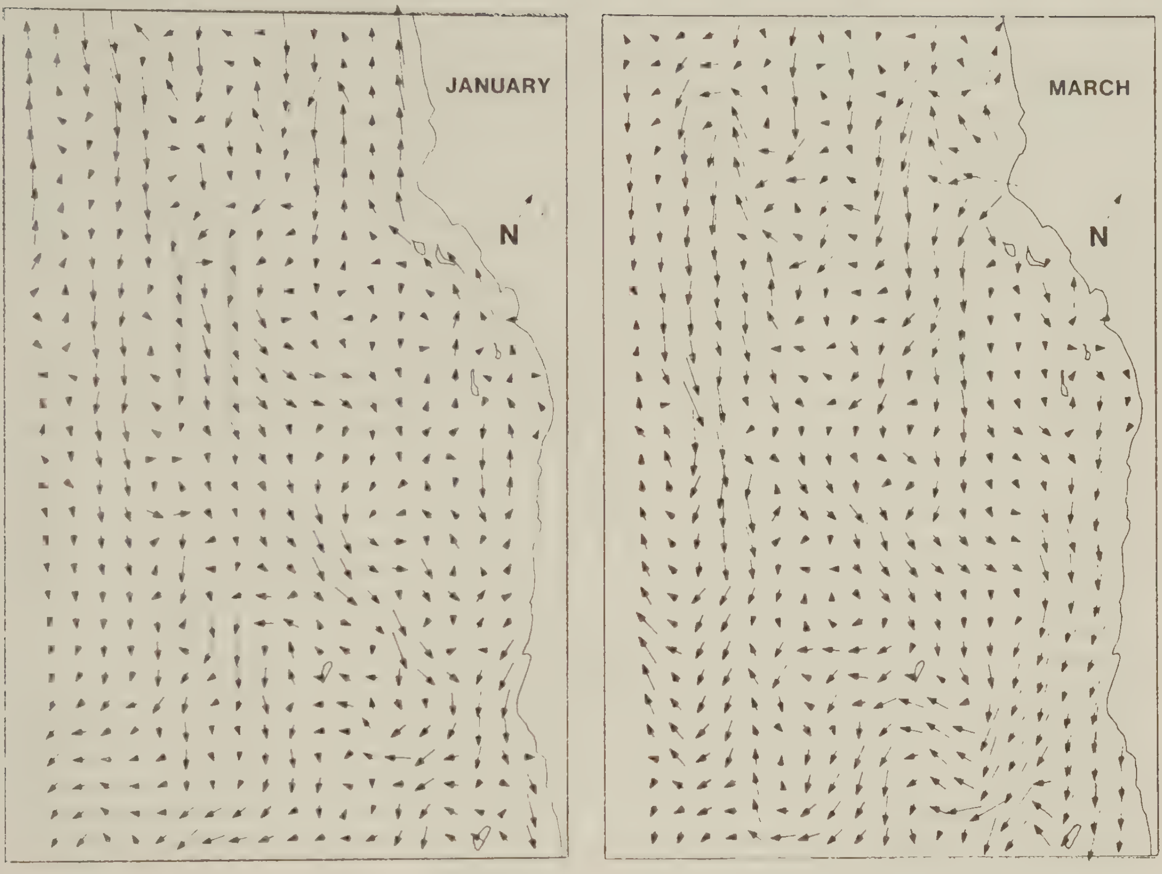


FIGURE 2.—Resultant mean current vectors for the normal January and the March seasonal current data used in this study. See text for cautions concerning figure interpretation. Length of arrow indicating north direction corresponds to a current velocity of 10 cm/s.

producing offshore directed Ekman transport. Two current fields were obtained by increasing the cross-shore component of the mean March Ekman velocities by the factors 1.5 and 3.0, and then combining the April seasonal geostrophic and augmented March Ekman velocities. Wind stress, and hence transport, is proportional to the square of wind speed. This means that roughly a 22% increase in a downshore wind speed increases the corresponding offshore directed Ekman transport by the factor 1.5. A threefold increase in offshore Ekman transport results from about a 77% increase in the downshore wind speed. Bakun and Nelson (1976) presented extensive statistical analyses of an "upwelling index" (defined as the offshore directed component of Ekman transport) for the location lat. 33°N, long. 119°W (this point is very close to location A used in the simulations; see below). Over an annual cycle the mean upwelling index for this location changes by at least a factor of two, with a rapid increase in both mean and standard deviation during the spring. The March mean index at this point was about 50 t/s per 100 m of coastline with a standard deviation of roughly 80, hence upwelling at this particular time and location can be highly variable. Further, Bakun and Nelson (1976) found that enhanced or diminished upwelling persists on a seasonal time scale, so incorporation in the model of prolonged increased Ekman transport was not unrealistic.

Diffusion was incorporated into the model solely to parameterize subgrid scale mixing; including larger scale and more ephemeral mixing processes would obscure the broad seasonal trends the model was intended to illustrate. The eddy diffusivity parameter was computed using scale-dependent diffusion formulae of Okubo (1976) and a regression analysis of diffusion data presented by Okubo (1971). The finite-difference representation of diffusion required the use of a pseudo-Fickian diffusivity coefficient, so the mean scale-dependent diffusivity for the 37 km grid spacing ($K_x = K_y = 101$ m^2/s) was used for all locations and all times in the model. The numerical method incorporated diffusion as the weighting factor $\coth[(uh)/(2K)]$ for the flux at each grid cell interface, where u is the current velocity at the interface and h is the 37 m grid spacing (see Power 1984 for further details). Hence, diffusion becomes important in regions of low current velocity, and at higher velocities diffusion is less important and advection dominates the flux. For the current velocities in most of the modeled region, the above hyperbolic cotangent function is usually evaluated to a magnitude near unity, making the contribution of turbulent transport to larval drift minimal relative to advective (current velocity) transport.

Simulations were carried out by starting an initial point source of northern anchovy eggs or larvae at various locations historically known to be larval anchovy habitat (Hewitt 1980). Examples of simulations for four starting locations (Table 1; Fig. 1), which are representative of the overall patterns produced by the simulations, are presented here. The four locations will be referred to in the text by their letter designations indicated in Figure 1 and Table 1. Northern anchovy larvae begin to school at about 27 d (Hunter and Coyne 1982); therefore larval distributions after 30 d of drift are presented. Thirty-d-old larvae are also rapidly increasing their "patchiness" (Hewitt 1981a), indicating that they could then exert significant control over their position. The time step in the simulations was 1 d. Results from a simulation using the actual northern anchovy egg distribution found in 1982 as the initial condition can be found in MacCall (1983).

TABLE 1.—Geographic and CalCOFI coordinates of starting locations for simulations presented in this paper. Letter designation corresponds to the same locations in Figure 1.

Starting location	Coordinates		CalCOFI	
	Lat. N	Long. W	Line	Station
A	33°08.4′	118°51.4′	89.17	42.5
B	32°54.1′	117°47.3′	92.5	32.5
C	31°59.3′	118°05.4′	95.83	42.5
D	32°14.1′	119°09.2′	92.5	52.5

Northern anchovy larval concentrations in the contour plots are relative to starting concentration; the unitless contour value of 10^{-2} represents a larval concentration two orders of magnitude below the starting concentration, and only concentrations down to 10^{-7} are illustrated. Larvae were permitted to be advected out the borders of the modeled area, except for the border along the coast. Grid cells bordering the Santa Barbara Channel (at about lat. 34°N, long. 120°W; Fig. 1) between the Channel Islands and Point Conception were open, and larvae advected into this region were considered to be lost from the system. Larvae were not permitted to be transported across any of the islands in the modeled region. Because March is the peak spawning time of northern anchovy, the effects of different starting locations on the 30-d larval distributions during March conditions will be presented first. The effects of spawning in different seasons and enhanced offshore Ekman transport during March will then be presented for comparison. The simulation results nominally represent larval northern anchovy distributions, but the results also apply to any planktonic species that begin drift at the same locations and maintain themselves in the top 50 m of the California Current.

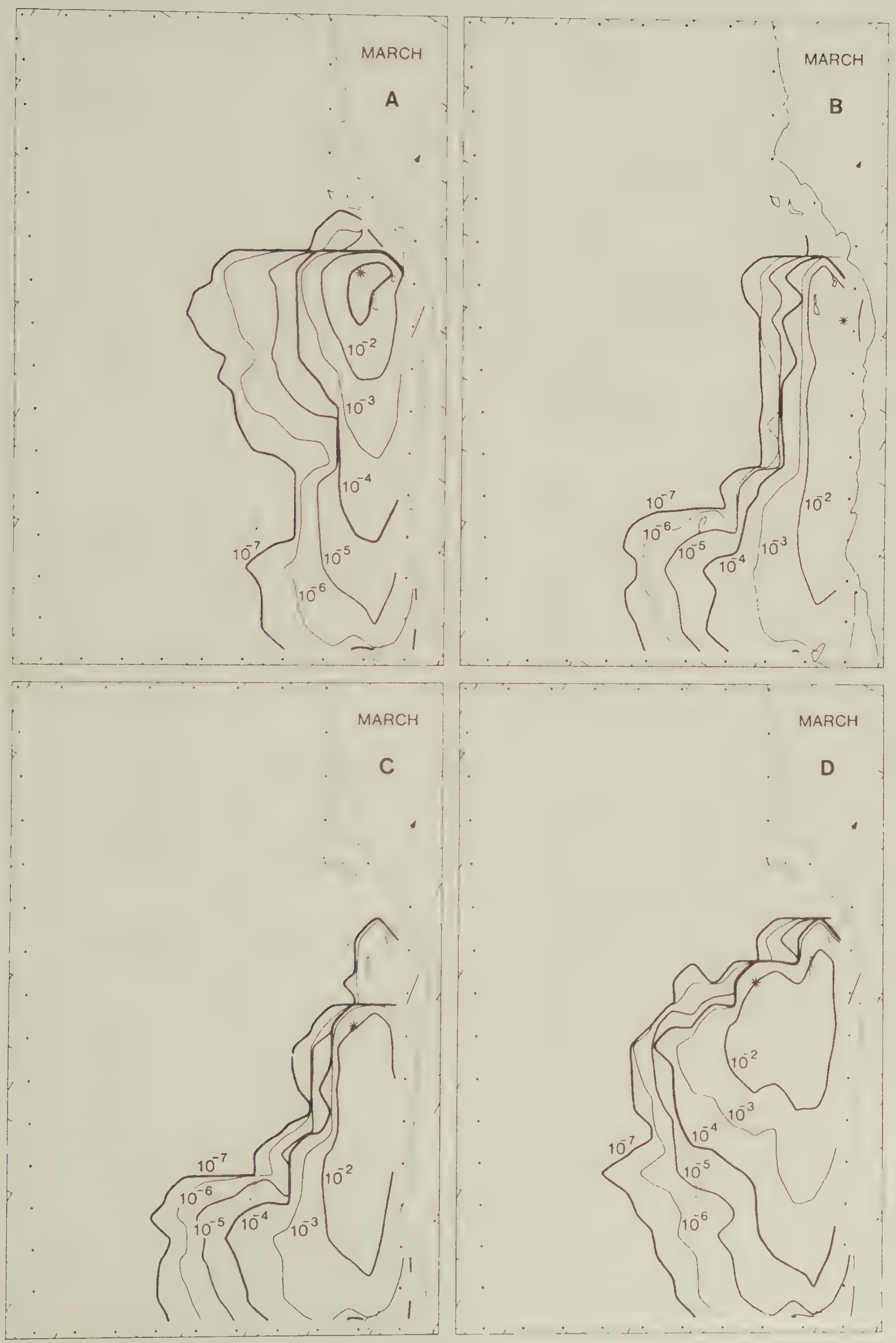
The overall extent of onshore-offshore and alongshore transport was of major interest in this study. A convenient way of summarizing the simulated larval distributions relative to their cross-shore distribution was to sum all larval concentrations in the cells having the same CalCOFI station coordinates. These sums were converted to percentages of the total number of larvae at 30 d, and the cumulative percentage of larvae present as one progressed offshore was plotted versus CalCOFI station coordinates. A similar procedures using CalCOFI line coordinates was done to summarize alongshore transport.

RESULTS

Effects of Starting Location, Normal March Currents

Northern anchovy larvae that began drift at location B, near the coast, were transported downshore by March currents (Fig. 3B). This was an effect of the nearshore southeasterly current (Fig. 2), and because of this flow only 15% of the larvae were at or upshore of the starting location after 30 d of drift

FIGURE 3.—Distribution of northern anchovy larvae after 30 d of drift in March currents. Letter designation corresponds to a simulation with northern anchovy begun at the corresponding lettered location in Figure 1 and Table 1; starting location is marked in this and subsequent contour plots with asterisks. Locations A and C share the same CalCOFI station coordinate; points B and D have the same CalCOFI line coordinate. Concentration contour intervals are proportions of the starting concentration, decreasing in order of magnitude steps. Tic marks around perimeter are at whole degrees of latitude and longitude; dots are at intervals of 3.33 CalCOFI line units from lines 70 to 120 and intervals of 10 station units offshore to station 120 (i.e., every 74 km).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(Fig. 4). The alongshore distribution of larvae below the starting point was quite uniform, and the lower larval concentrations had reached the southern border of the modeled region (CalCOFI line 120). Dispersal offshore was minimal, and a majority of the larvae lay in a band near the coast with about equal proportions inshore and offshore of the starting point; 92% of the larvae were on or inshore of CalCOFI station 37.5. After initial southeasterly transport, some larvae were transported in an offshore, southwesterly direction.

Extensive downshore transport also occurred to northern anchovy larvae begun at location C, and in fact only 3% of the larvae remained at or upshore of the starting location after 30 d of drift (Figs. 3C, 4). The larvae begun at point C were also concentrated in a narrow band along the coast, but unlike those started at point B most of the larvae begun at C moved inshore of the starting location after 30 d of drift.

Northern anchovy larvae begun at the offshore location D showed much less extensive downshore transport than those begun at B or C (Figs. 3D, 4). Only 10% of the larvae remained at or upshore of the starting point, but 86% of the total remained at or between CalCOFI line 92.5 (location C's line coordinate) and line 102.5, a span of 222 km. Most larvae were inshore of location D, and the cross-shore distribution was slightly more uniform than those begun farther inshore. Starting point D's distance from the coastline permitted the slightly broader cross-shore distribution.

Larvae begun at location A showed an alongshore cumulative percentage distribution after 30 d of drift which was similar to that of larvae that begin drift at point D, although it was displaced farther upshore (Fig. 4). Location A produced the greatest percentage of larvae remaining at or upshore of the starting location, and there is a small patch of high (10^{-1}) larval concentrations present at the starting location (Fig. 3A). This reduced dispersal of larvae begun at A also produced the strongest cross-shore gradient of larvae. A majority of the larvae were again on or inshore of the starting location after 30 d of drift.

In summary, the distributions of northern anchovy larvae that began drift at locations A through D and that were produced by March currents were formed as relatively strong cross-shore gradients, so that the 30-d distributions were bands (ca. 100 km wide) parallel to the coast. The results of starting larvae at locations A, C, and D were that more than 85% of the larvae were inshore of the starting location after 30 d of drift. Larvae that began drift at locations B and C were extensively carried downshore of the starting location. Most of the larvae that started at points A and D also moved downshore from those locations, but the bulk of the larvae were not as widely dispersed from the starting location as those begun at points B and C.

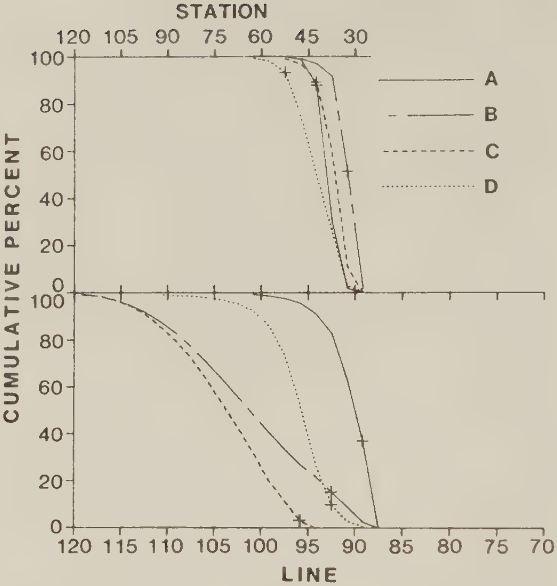
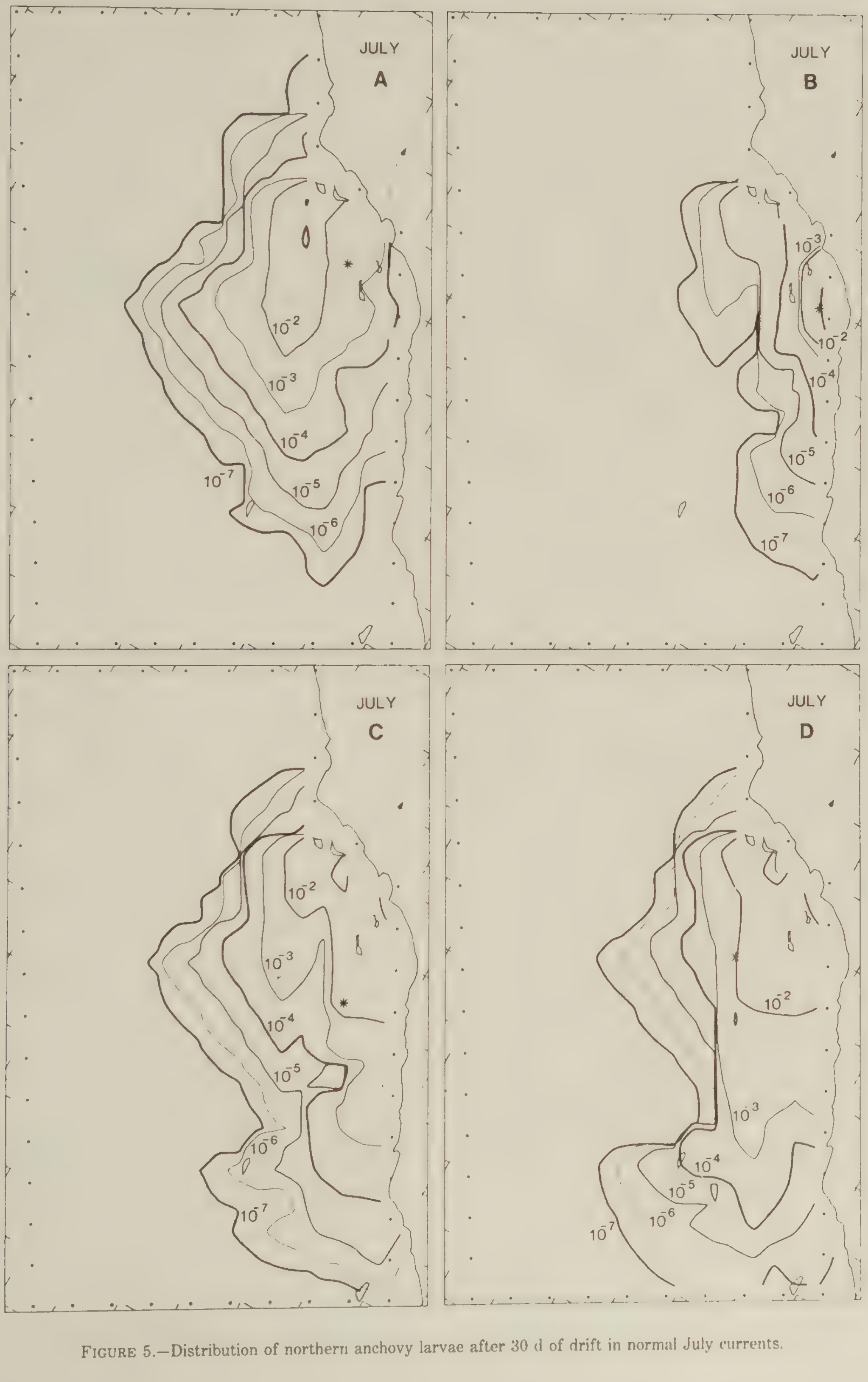


FIGURE 4.—Cumulative percentages of northern anchovy larvae after 30 d of drift, progressing offshore (increasing CalCOFI station number) and downshore (increasing CalCOFI line number), for the four starting locations under March current conditions. Cross symbols are at the starting location's corresponding CalCOFI line or station coordinate. Distance between tic marks on the abscissae is equivalent to a distance of 111 km. Note that a steep curve implies a compact distribution of larvae, while more gradual slopes imply more widely dispersed larvae.

Effects of Seasonal Current Fields on Larval Distribution

The distributions of northern anchovy larvae started at the same location but using different seasonal current regimes appear very different to the eye (Figs. 3, 5-7). Part of this effect is real, but part is also due to displacement of the contours for the lower larval concentrations (e.g., 10^{-7}), which represent few larvae. The cumulative percentage plots (Fig. 8) indicate that, when summarized on a model-wide basis, the overall cross-shore distributions of larvae begun at locations B, C, and D were not greatly different when currents from the four seasonal periods were used in the simulations. A fixed distance offshore there were some large differences in the cumulative percentages among seasons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10^{-6}
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JULY
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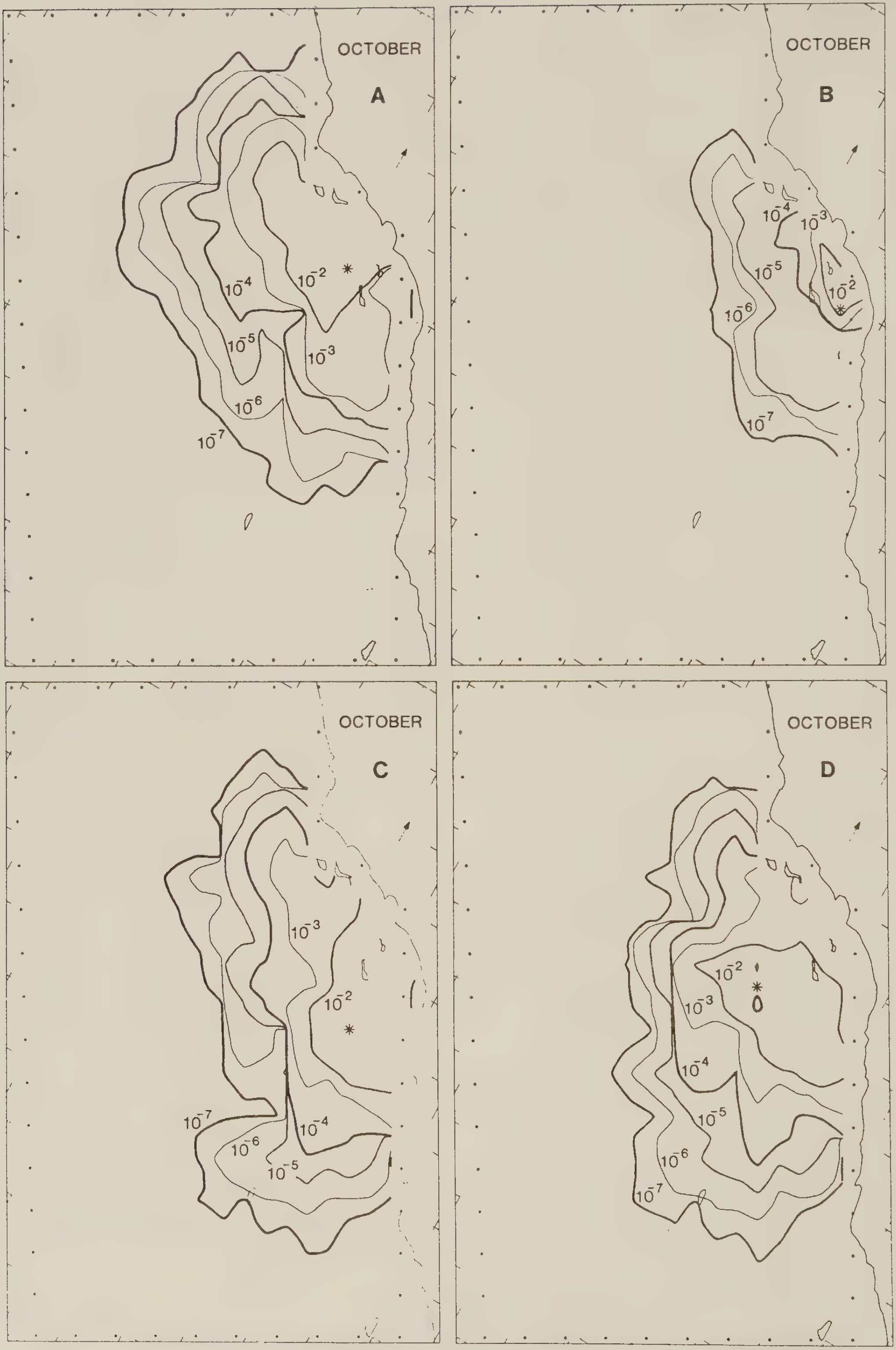
FIGURE 5.—Distribution of northern anchovy larvae after 30 d of drift in normal July currents.


OCTOBER
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OCTOBER
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FIGURE 6.—Distribution of northern anchovy larvae after 30 d of drift in normal October currents.

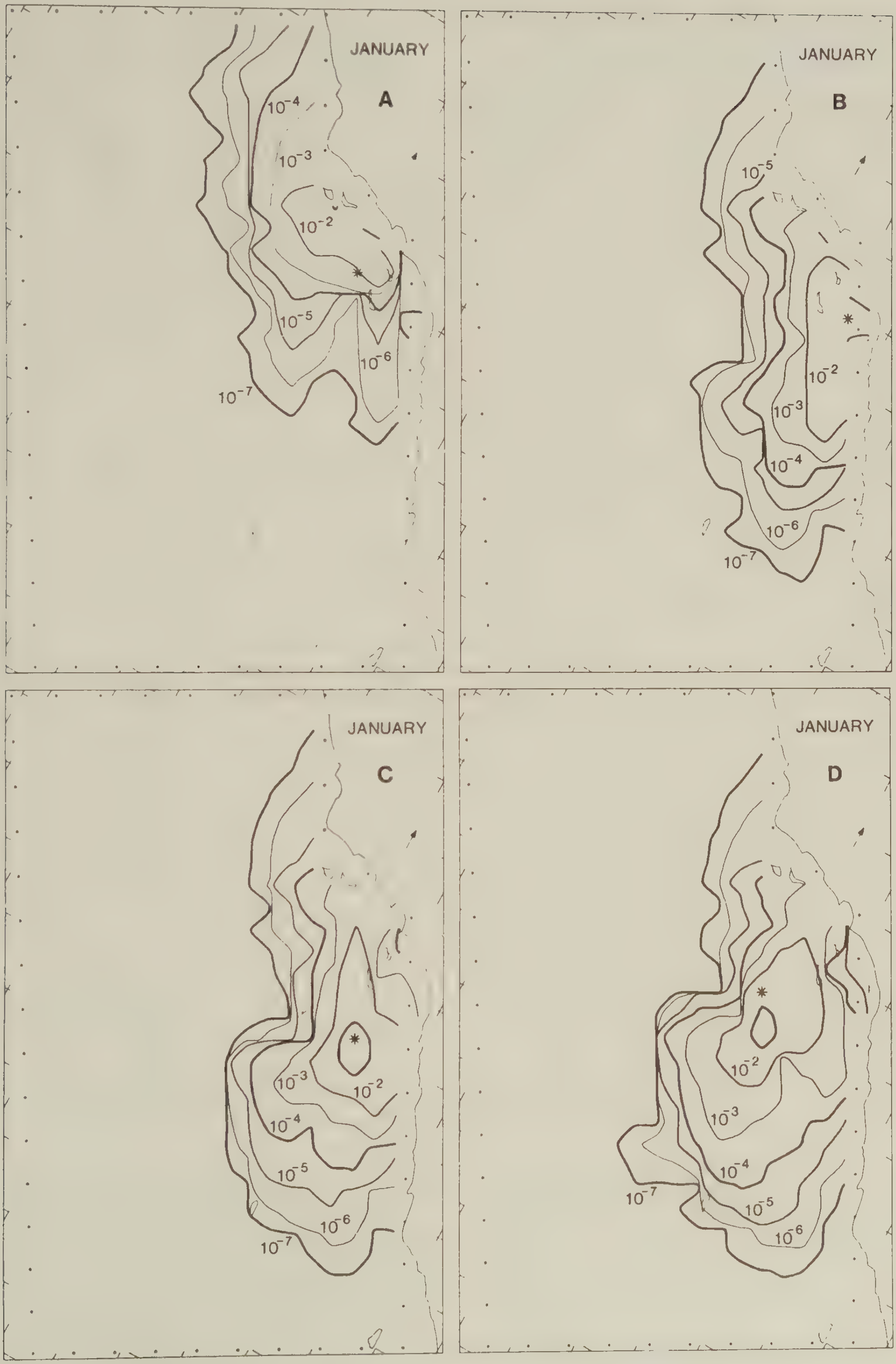
JANUARY
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FIGURE 7.—Distribution of northern anchovy larvae after 30 d of drift in normal January currents.

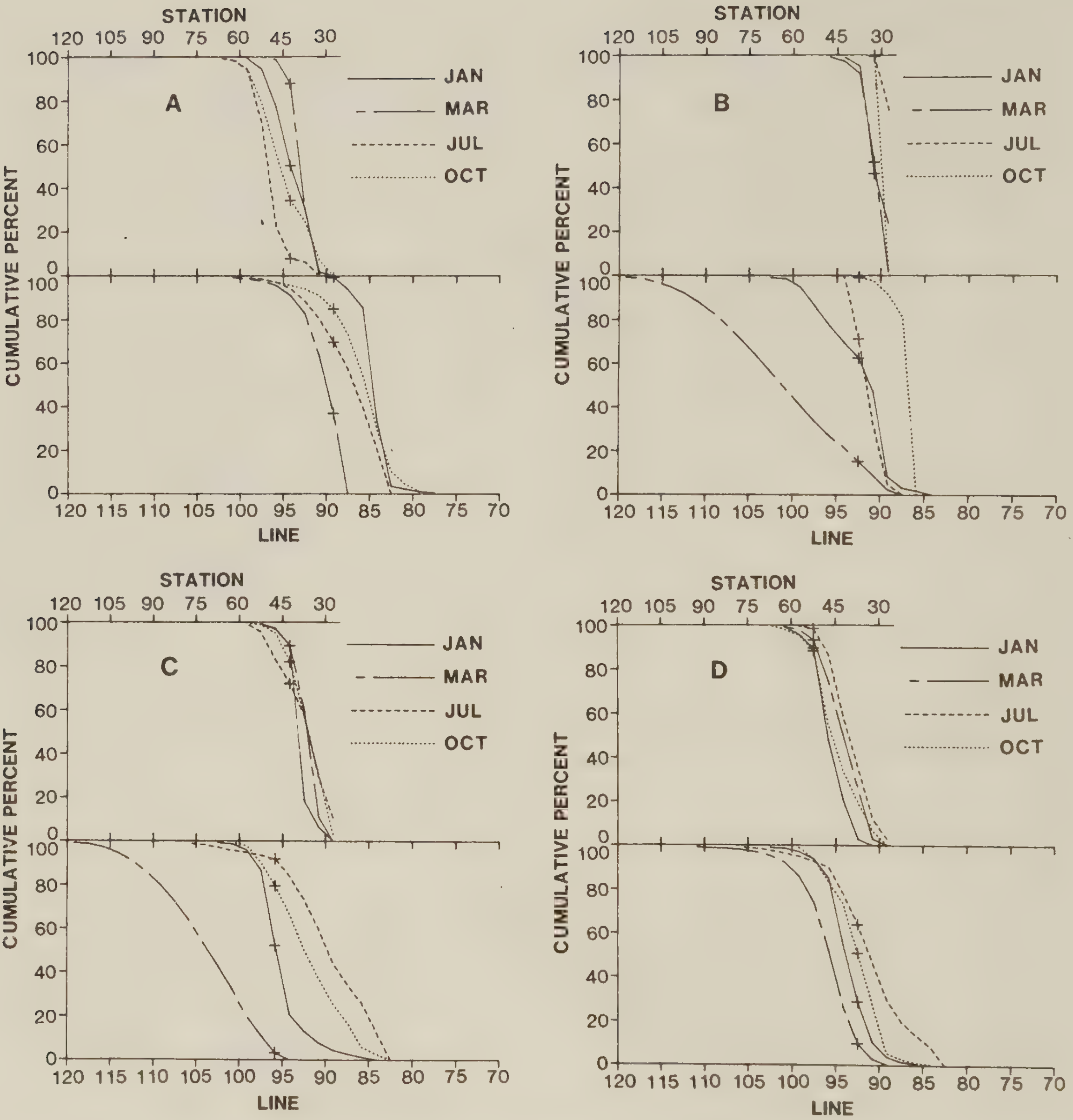


FIGURE 8.—Cumulative percentage plots of northern anchovy larval concentrations after drift in the four seasonal current regimes. Letter designation corresponds to starting locations indicated in Figure 1 and Table 1.

for larvae begun at the same location, but a comparable percentage was usually present a short distance away, i.e., most curves in Figure 8 are closely spaced on the CalCOFI station abscissae. Most larvae begun at the offshore location D moved inshore regardless of season, and the seasonal differences were in the relative extent of inshore movement, the maximum occurring during July. In all simulations the cross-shore distributions of larvae formed strong gradients, regardless of season.

Starting location A is within the Southern California Bight proper, the region that most consistently has high larval concentrations of northern anchovy (cf. Hewitt 1980). Larval distributions started at location A did exhibit notable seasonal differences in their 30-d cross-shore distributions, with the greatest offshore dispersal occurring during July (Figs. 5A, 8A), and the largest inshore movement occurring during March current conditions (Figs. 3A, 8A). January and October were intermediate between these two extremes. In all cases the cross-shore gradients of larvae were strong.

In contrast, the alongshore distributions of larvae differed markedly when the simulations were done with currents from the four seasonal periods. Virtually all larvae were carried upshore of starting location A by the California Countercurrent in the January simulation (Figs. 7A, 8A), but when the model was run using March currents, a majority of the larvae were downshore of point A after 30 d of drift (Fig. 3A). The July and October simulation results for point A seemed to indicate an annual progression between the March and January extremes (Fig. 8A).

The seasonal differences in the overall alongshore distributions were even more dramatic for northern anchovy larvae begun at locations B and C. The uniform downshore distribution produced by March currents differed from the distributions formed in all other seasons. Larvae begun at location B were all transported upshore of the starting location during October current conditions (Fig. 6B). When January currents were used (Fig. 7B), the upshore movement had lessened, so that only 62% of the larvae were at or upshore of location B, and the larvae were more evenly distributed along the coast (Fig. 8B). March currents yielded the greatest downshore movement, and the July distribution (Fig. 5B) was intermediate between that produced by March and October conditions, with the alongshore gradient of larvae again steepening. The changes on an annual basis between upshore, then downshore transport were similar for larvae begun at location C, except that the July current conditions produced the greatest upshore transport (Figs. 5C, 8C); March again produced the maximum downshore transport for larvae begun at point C (Fig. 3C). Larvae begun at location C formed a relatively compact distribution after 30 d of drift in the January currents (Fig. 7C).

The overall alongshore distributions of northern anchovy larvae that started drift at point D appeared to be least influenced by seasonal changes in the currents, although March conditions again produced the greatest transport downshore of the starting point (Fig. 3D), with July currents again yielding the greatest upshore transport (Fig. 5D). January currents also produced a very compact distribution of larvae started at location D, similar to that of larvae begun at point C.

In summary, only northern anchovy larvae begun at location A appeared to have notable differences in their model-wide, cross-shore distributions after 30 d of drift. Larvae begun at all four locations did have substantial seasonal differences in their alongshore distributions, with March currents consistently producing the greatest downshore dispersal. The least downshore dispersal occurred during January, October, July, and July current conditions for larvae started at locations A, B, C, and D respectively. January currents generally seemed to produce the most compact 30-d distributions of larvae (least dispersal).

Effects of Increased Offshore Ekman Transport, March Currents

Increasing the March cross-shore Ekman transport by a factor of 1.5 had little effect on the 30-d distributions of northern anchovy larvae begun at locations B and C (Fig. 9); these curves are also closely spaced on the CalCOFI station abscissae. Increasing the average or "normal" offshore Ekman component by a factor of three produced more noticeable changes in the cross-shore distributions of larvae begun at points B and C, but this effect was not substantial; the contours representing the lower concentrations extended far offshore (Fig. 10B, C), but the higher concentration contours, which delimit the majority of the larvae, were not greatly displaced from those of normal March currents (Fig. 3B, C). This is also evident in the cumulative percentage curves.

In comparison, northern anchovy larvae begun at locations A and D underwent about the same increase in offshore dispersal with a 1.5× offshore directed Ekman component increase as those begun at points B and C did with the 3× offshore Ekman increase (Fig. 9). When the offshore directed Ekman transport was increased to three times its normal mean value, the effects on larvae begun at points A and D were substantial. A majority of the larvae were carried offshore of starting locations A and D, and a large fraction were transported a significant distance (Fig. 10A, D), well seaward of the Southern California Bight. The increase in offshore Ekman transport also noticeably affected the alongshore distributions of larvae begun at locations A and D (Fig. 9). The overall pattern of alongshore distribution is similar to that produced by the normal mean conditions, but the larvae were generally farther downshore.

DISCUSSION

Models have inherent assumptions and simplifica-

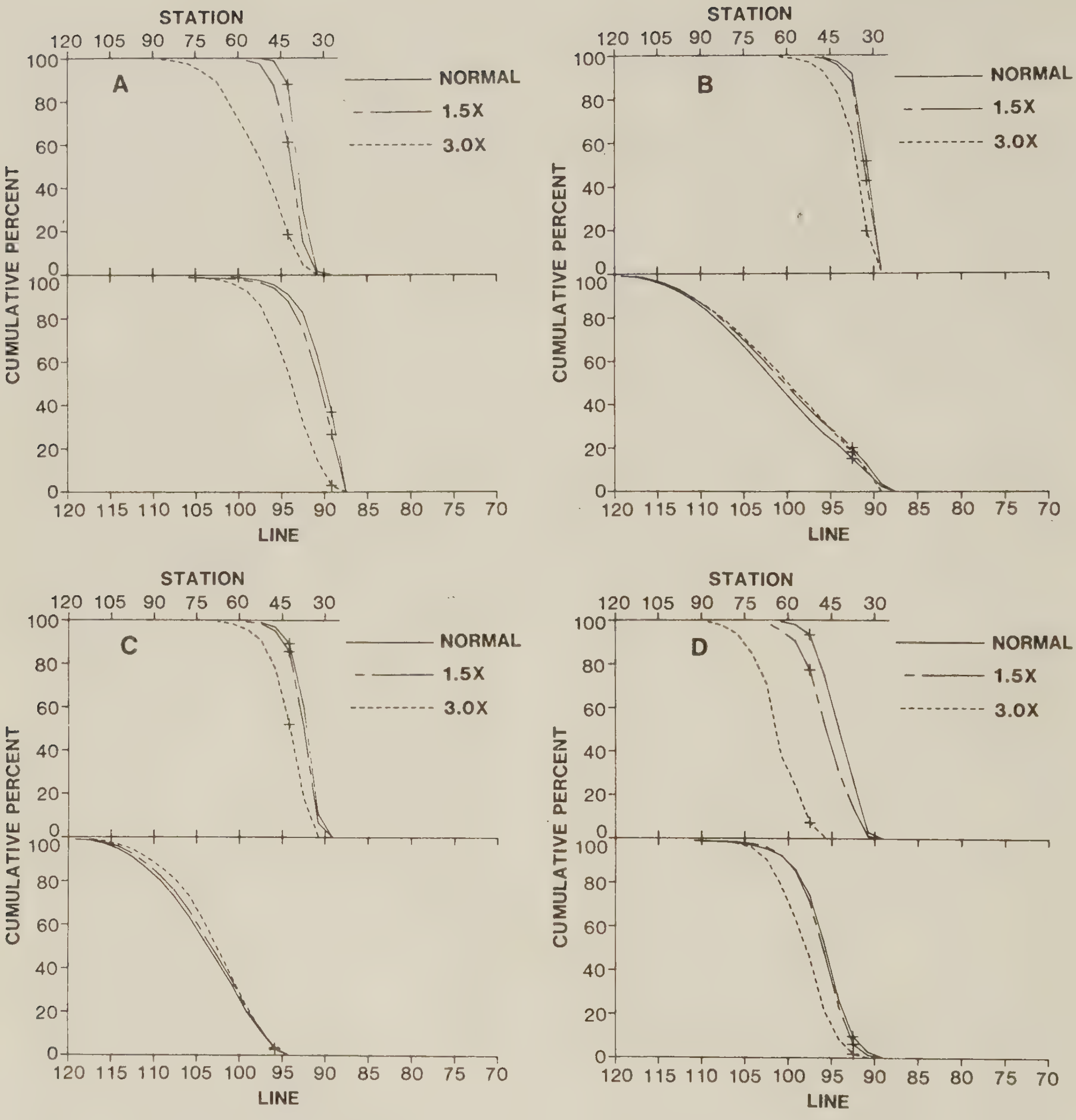
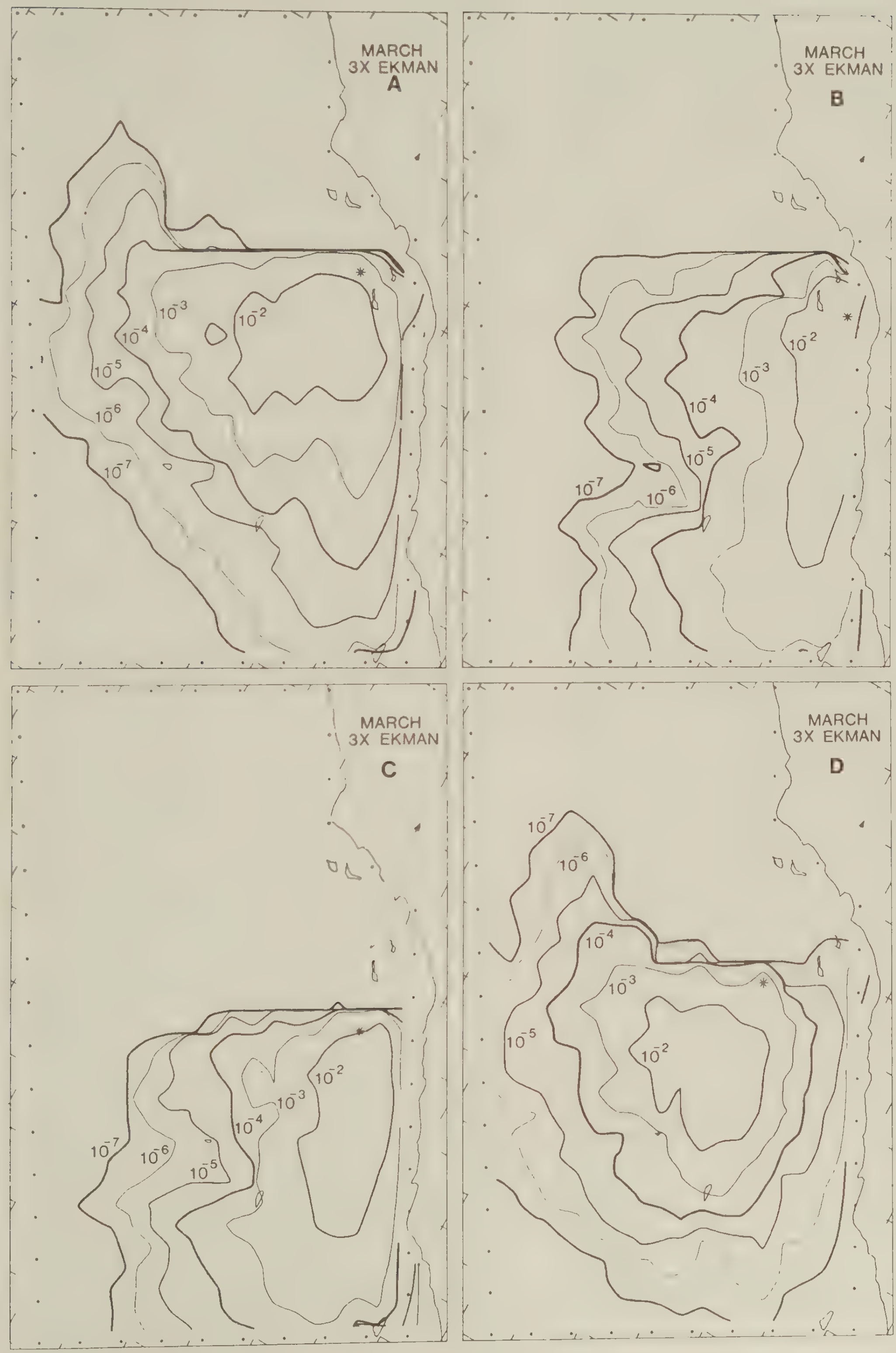


FIGURE 9.—Cumulative percentage plots of northern anchovy larval concentrations after 30 d drift in the three March Ekman current regimes ("normal" or long-term mean, 1.5× offshore directed Ekman transport, 3× offshore directed Ekman).

tions, and thus approximate what occurs in nature. The geostrophic current information, while some of the best available, nonetheless constrained the spatiotemporal resolution of this model, and incorporating Ekman transport required several assumptions. Further, there can be considerable interannual variability in the modeled region (Mooers and Robinson 1984; Simpson et al. 1984), and presumably the model is of "average" conditions and cannot be representative of any specific year; I felt that including such variability (assuming adequate data were available) would complicate the results without significantly contributing to biological insight. An

FIGURE 10.—Distribution of northern anchovy larvae after 30 d of drift in March currents with three times the normal offshore directed Ekman transport.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MARCH
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C
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MARCH
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additional confounding factor is the lack of biological information in the model; consistent larval behavior patterns (e.g., diurnal vertical migrations) and spatially heterogeneous mortality could produce distributional patterns differing from those presented here. In spite of these caveats, the simulations do demonstrate that variations in northern anchovy spawning location and time, and changes in the magnitude of offshore directed Ekman transport, can have significant consequences for the subsequent larval distribution. By inference, these changes in distribution can result in increased or reduced larval mortality, and ultimately affect adult northern anchovy population size.

Offshore transport was not significant in the simulations done with the unaugmented or "normal" March (seasonal April geostrophic + March Ekman) currents. A majority of the northern anchovy larvae that began drift at the four starting locations were inshore of their starting points after 30 d of drift, and the cross-shore distributions indicated that most larvae occupied a relatively narrow range of distances close to shore. Mais (1974) and Methot (1981) reported that most juvenile northern anchovy occupy inshore areas in the fall, and the model indicates that this inshore movement could be facilitated by passive drift. As mentioned earlier, the consensus is that nearshore regions provide more hospitable food conditions for the northern anchovy larvae. Lasker (1978, 1981) summarized the results of surveys of larval food distributions in the Southern California Bight. His figures indicate that suitable larval food concentrations decline rapidly as one progresses offshore. O'Connell (1980) reported the results of a survey for starving northern anchovy larvae in the Southern California Bight, the degree of starvation being defined by histological criteria. He found apparently healthy larvae at locations as far as about 250 km offshore (at lat. 32°30′N, long. 120°W), where model concentrations were $<10^{-7}$ after 30 d in all March simulations except for larvae begun at A, where they were $<10^{-4}$. Despite the good condition of these offshore larvae, the simulation results indicate a low likelihood of their being recruited to the nearshore juvenile population. The low offshore larval concentrations will also hinder the development of schooling (Hewitt 1981a).

The minimal offshore transport situation found in the March current simulations was also generally true when simulations were done using currents from other seasons, except for northern anchovy larvae begun at location A. This point is the most interior starting location within the Southern California Bight proper and is primary northern anchovy spawning habitat (Hewitt 1980) and where seasonal changes in the currents are especially important (Tsuchiya 1980). Spring is a time when currents in the Southern California Bight are not as well organized as other times of the year, and the Southern California Eddy is often absent (Hickey 1979; Owen 1980). It is interesting that currents during March, the peak spawning period, produced the least offshore transport of larvae begun at location A when compared with other seasons, even though March is the time of greatest overall Ekman transport (Bakun and Nelson 1976). There is significant spawning in January (Methot 1981), and the January simulations also had reduced dispersal of larvae. The model results support the hypothesis of Parrish et al. (1981) that northern anchovy spawning in the Southern California Bight do so at a time and place that minimizes offshore transport of eggs and larvae.

It is clear that the overall 30-d alongshore distributions of northern anchovy larvae produced by normal March currents depended largely on the spawning location's proximity to the well-defined southeasterly current present near the coast in the southern half of the modeled region. Larvae that started drift near this current underwent extensive downshore transport. Larvae begun farther into the Southern California Bight (location A), and farther offshore (location D), were also transported downshore, but to a much lesser extent. This again confirms the role of the Southern California Bight as an area where minimal transport of spawning products takes place. The southwesterly, offshore transport that occurred in many of the simulations at the southern margin of the modeled region (between CalCOFI lines 110 and 120) is consistent with the evidence that this region forms a faunal boundary between species of the Southern California Bight and those of Baja California to the south, and that this faunal boundary is created by current patterns (Hewitt 1981b). This is also a region of increased surface convergence (Parrish et al. 1981).

The extent of alongshore transport was markedly different for northern anchovy larvae begun at the same starting location when currents from the different seasons were used. Depending on starting location, seasonal changes in currents could produce almost complete reversals between predominantly upshore or downshore transport. March currents consistently produced the greatest downshore transport. These effects were due to the presence or absence of the Southern California Eddy and the Southern California Countercurrent. Because the Southern California Countercurrent is present year-round, except during peak spawning in the spring, it is clear that the relationship between the time of northern anchovy spawning and the time that this countercurrent diminishes is critical. The simulations indicated that eggs and larvae from early spawning (i.e., January) are carried upshore into the Santa Barbara Channel and north of Point Conception, while those from later spawning (March) move in the opposite, southeasterly direction. The sizes and birth dates of juveniles collected in the fall of 1978 and 1979 were in accordance with this pattern. Methot (1981) reported that juvenile northern anchovy collected during both fall seasons in the northern portion of the Southern California Bight had birth dates (as determined from daily growth increments in otoliths) in the preceding months of December and January, and these fish were generally larger than those collected farther to the south. The northern anchovy collected in the south had predominantly February and March birth dates. It may be that the northern group, containing fish from early spawning, were advected to the north by the Southern California Countercurrent and that the southern group of fish from late spawning were produced when the surface countercurrent had diminished. Future studies of the transport and distribution of northern anchovy larvae or other planktonic species in the Southern California Bight should incorporate as much information as is available on the presence and magnitude of the Southern California Countercurrent and the Southern California Eddy.

Nearshore winds in the Southern California Bight are relatively weak, and downshore wind speeds generally increase farther offshore (Bakun and Nelson 1976; Nelson 1977; Dorman 1982). The implication, in terms of offshore transport, is that larvae closest to shore are affected least by offshore transport, while those farther offshore experience a much greater impact. Thus the areal extent of northern anchovy spawning interacts with offshore Ekman transport; in years when most northern anchovy spawn close to shore there will be decreased offshore transport, because of weak inshore winds, than in years when northern anchovy spawn farther offshore. The impact on the products of offshore spawning will depend on the magnitude of the winds in the offshore areas in each particular year. Northern anchovy larvae that began drift farthest north in the Southern California Bight (location A) and at the more offshore location (D) were most affected by increases in offshore directed Ekman transport, indicating southerly and inshore spawning are best for reduced dispersal in March. Hewitt and Methot (1982) stated that the area of northern anchovy spawning was more compact and more northerly in 1978 than in 1979. Survival of young larvae was about the same in both years, indicating that early mortality from starvation and predation was not substantially different in the two years. Survival through the juvenile stage was greater in 1978 than in 1979, however, and Hewitt and Methot (1982) cited increased offshore transport in 1979 as a possible reason.

Superimposed on the effects of spawning location is the interaction between the increase in downshore wind speeds (offshore directed Ekman transport) as one progresses offshore and the magnitude of interannual variations in the wind speeds. In the simulations the effects of the 3× increase in Ekman transport were substantially greater than those of the 1.5× increase. The 1.5× change was not a great enough increase to carry many northern anchovy larvae into offshore regions of higher, offshore directed Ekman transport. The inshore 3× increase carried a greater fraction of larvae farther offshore, and the 3× increase in the offshore region subsequently operated on a greater proportion of the larval population. Thus there was an interaction between enhanced offshore directed Ekman transport in the nearshore area and increased Ekman transport farther offshore, the two of these acting together to produce the extensive drift evident in the simulation results. Years in which downshore winds increase in only the inshore or the offshore regions would not produce as much overall offshore dispersal. Bakun and Nelson's (1976) statistical analyses of the "upwelling index" indicates that prolonged increased Ekman transport is feasible, although the 3× condition would probably be a particularly bad year. It should also be noted that Ekman transport was incorporated into the model as acting uniformly on the 50 m surface layer, and presumably the model depicts the drift of "average" larvae. Larvae that remain near the surface or at 50 m would undergo greater or lesser transport, respectively. Alternatively, it is known that winds in the Southern California Bight have a strong diurnal periodicity (Bakun and Nelson 1976; Dorman 1982), and a diurnal vertical migration coupled with diurnal changes in the winds could significantly alter larval drift.

In summary, the simulation results indicated that seaward dispersal of northern anchovy larvae is generally small, but that seasonal effects are strongest in the area of peak spawning (location A) and that March spawning at this point minimizes offshore dispersal. Spawning at locations or times near well-defined currents, such as the California Countercurrent, can produce major changes in larval distribution, and consequently may affect larval survival. The effect of offshore directed Ekman transport on the larval population depends on the areal extent of northern anchovy spawning, and the spatial distribution of any changes in wind stress and subsequent Ekman transport; an increase in Ekman transport in both the inshore and offshore regions will act together to produce maximum offshore dispersal.

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AN INTENSIVE FISHING EXPERIMENT FOR THE CARIDEAN SHRIMP, *HETEROCARPUS LAEVIGATUS*, AT ALAMAGAN ISLAND IN THE MARIANA ARCHIPELAGO

STEPHEN RALSTON[1]

ABSTRACT

During January 1984 an intensive fishing experiment for the deepwater caridean shrimp, *Heterocarpus laevigatus*, was conducted near Alamagan Island in the Mariana Archipelago. Twenty standard shrimp traps were set daily, producing a significant decline in the average catch rate from 3.33 to 1.82 kg/trap-night over a 16-day period. This drop was associated with a removal of 776 kg of shrimp from the study site. Resampling the area 4 months later showed that the catch rate remained depressed. Length-frequency data demonstrate that the decrease in catch per unit effort was due to a decline in the number of shrimp caught. An initial population size of 1,714 kg from 312 ha habitat is estimated, corresponding to one exploitable shrimp per 51 m^2. The estimate of catchability (0.001945 trap-night^{-1}) indicates that *H. laevigatus* may be easily overfished by trapping.

Intensive fishing experiments can provide the ideal complement to resource surveys using catch per unit effort (CPUE) to estimate the relative abundance of exploitable stock. Whereas values of CPUE are usually adequate for studying spatial and temporal variation in resource abundance, often an absolute estimate of exploitable biomass is required. This is particularly true of yield assessments. Due to the relative nature of CPUE statistics, a conversion factor is necessary to translate catch rates into absolute units of biomass. This proportionality is termed catchability, typically a constant parameter (but see Schnute 1983; Polovina 1986) which can be estimated from the results of intensive fishing experiments (Ricker 1975).

The advantages of intensive fishing over alternative methods of estimating the catchability coefficient (q) are several. Foremost is that no history of either catch or effort data is needed. This characteristic makes methods of fishing success (Ricker 1975) or survey-removal (Schnute 1983) particularly attractive for use in assessments involving exploratory survey data, as well as for studying emerging new fisheries. A second advantage is that results can be obtained rapidly. Because fishing is, by definition, conducted intensively over a short time period and the necessary computations are quite simple, an estimate of q is quickly realized.

Although these advantages recommend the approach, two restrictive assumptions must be made in analyzing the data. One must assume, in the absence of information to the contrary, that the population fished is closed, or equivalently, that additions exactly balance removals other than those due to fishing. The basis of this assumption can be strengthened if the intensive fishing site is located in a naturally isolated area. For example, Polovina (1986) performed an intensive fishing experiment on a small pinnacle 5.5 km in circumference which was isolated by 75 km of deep water from the nearest similar habitat. A second assumption is that fishing removals account for all changes in stock biomass, i.e., natural mortality, growth, and recruitment are negligible during the period of fishing. For this reason, removals are carried out intensively over as short a time interval as possible. If both assumptions hold then q can be estimated directly by the slope of the linear regression of either CPUE on cumulative catch (Leslie and Davis 1939) or log{CPUE} on log{cumulative effort} (DeLury 1947).

Refinements to these two basic methods have been proposed by Braaten (1969), Crittenden (1983), Schnute (1983), and Polovina (1986) among others. Generally, estimators have been found to be most sensitive to a departure from the assumption of constant catchability. A variety of adjustments have been used to correct this and other statistical problems which often occur with real data.

The work reported here is an application of the intensive fishing method to estimate the catchabil-

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[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

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ity and population density of a deepwater caridean shrimp, *Heterocarpus laevigatus*. This circumglobal species is found in depths of 400-950 m in subtropical and tropical latitudes (King 1984). Experimental trapping surveys have shown it to be abundant at widespread localities in the central and western Pacific (King 1983), and a developing commercial fishery for this species has emerged in the Hawaiian Islands (Gooding 1984). Interest by Pacific island nations in promoting the harvest of this shrimp is great (King 1981), providing the impetus for an assessment of the *Heterocarpus* resource in the Mariana Archipelago. Additional results of this research program are reported elsewhere (Moffitt and Polovina[2]).

MATERIALS AND METHODS

Intensive fishing for *Heterocarpus laevigatus* was conducted in an area 3.5 km off the north end of Alamagan Island in the western Pacific (lat. 17°39′N, long. 145°50′E). Alamagan is part of the Commonwealth of the Northern Mariana Islands, lying 450 km north of Guam (Fig. 1). It is small, uninhabited, and of recent volcanic origin. While the ocean bottom slopes steeply away from the island at an angle of 25° to the east, south, and west, a broad shelf, approximately 6.5 km^2 in area and lying 600-800 m deep, extends well off the north end of the island. This shelf was selected as a study site because 1) good catches of *H. laevigatus* were previously obtained in the area, 2) 700 m is an ideal target depth for trapping this species (Moffitt and Polovina fn. 2), 3) the relatively uniform bottom topography would facilitate setting and retrieving fishing gear, and 4) the area had no known history of prior exploitation.

Fishing was conducted over a 16-d period, 9-24 January 1984, from the NOAA ship *Townsend Cromwell*. Shrimp traps of standard Honolulu Laboratory design were set daily in four strings of five traps each. All traps were half round in shape (91 × 66 × 46 cm), with a frame constructed of 1.27 cm reinforcing steel, covered with 1.27 × 2.54 cm mesh hardware cloth (illustrated in figure 3 of Gooding 1984). Individual traps within a set were spaced 40 m apart and were baited with three chopped Pacific mackerel, *Scomber japonicus*. All traps were set between 1100 and 1300 h in 600-800 m and were retrieved the following day between 0800 and 1100 h. In addition, a large (150 × 150 × 150 cm) pyramidal commercial shrimp trap was sometimes deployed alone.

When fishing gear was recovered, the traps were individually emptied and the contents sorted, counted, and weighed to the nearest 0.01 kg by species lot. On three occasions a random length-frequency sample of trap-caught *H. laevigatus* was saved for later study. All shrimp in these samples were measured to the nearest 0.1 mm CL (carapace length) with dial calipers.

To accurately delimit the bottom topography of the study area, an unregistered reconnaissance hydrographic survey was conducted over the site on 9 February 1984, with the *Townsend Cromwell*. Depth soundings from a Raytheon[3] fathometer were recorded every 3 min over an 8.5-h period as the vessel ran a predefined cruise track which covered the entire study area. The position of the vessel was recorded to the nearest 0.01 min at each sounding.

The *Townsend Cromwell* returned to the study site again from 12 to 16 May 1984, to assess the recovery of the *H. laevigatus* population in the study area and to determine the effect of different baiting practices on CPUE. Four sets of six traps each were set overnight on each of four occasions. Half these traps contained three chopped Pacific mackerel whereas the other half (i.e., every other one) contained two whole Pacific mackerel. The catch was sorted and treated as discussed previously.

RESULTS

Hydrographic Survey

A total of 164 depth soundings were obtained over the study site. The data were contoured using the GCONTOUR procedure of SAS/GRAPH (SAS 1981) and the resulting chart is presented in Figure 2. Solid lines represent isobath contours spaced at 200 m depth intervals. Note that the shrimp study site is a saddle point; concave upwards along the north-south axis and concave downwards from east-west. The hydrographic survey revealed a small but steep pinnacle and a deep canyon immediately adjacent to the study area.

In the figure the locations of each string of five standard traps are shown as open circles ($n = 60$) whereas single sets of the large pyramid trap are given as closed circles ($n = 8$). Fishing effort was

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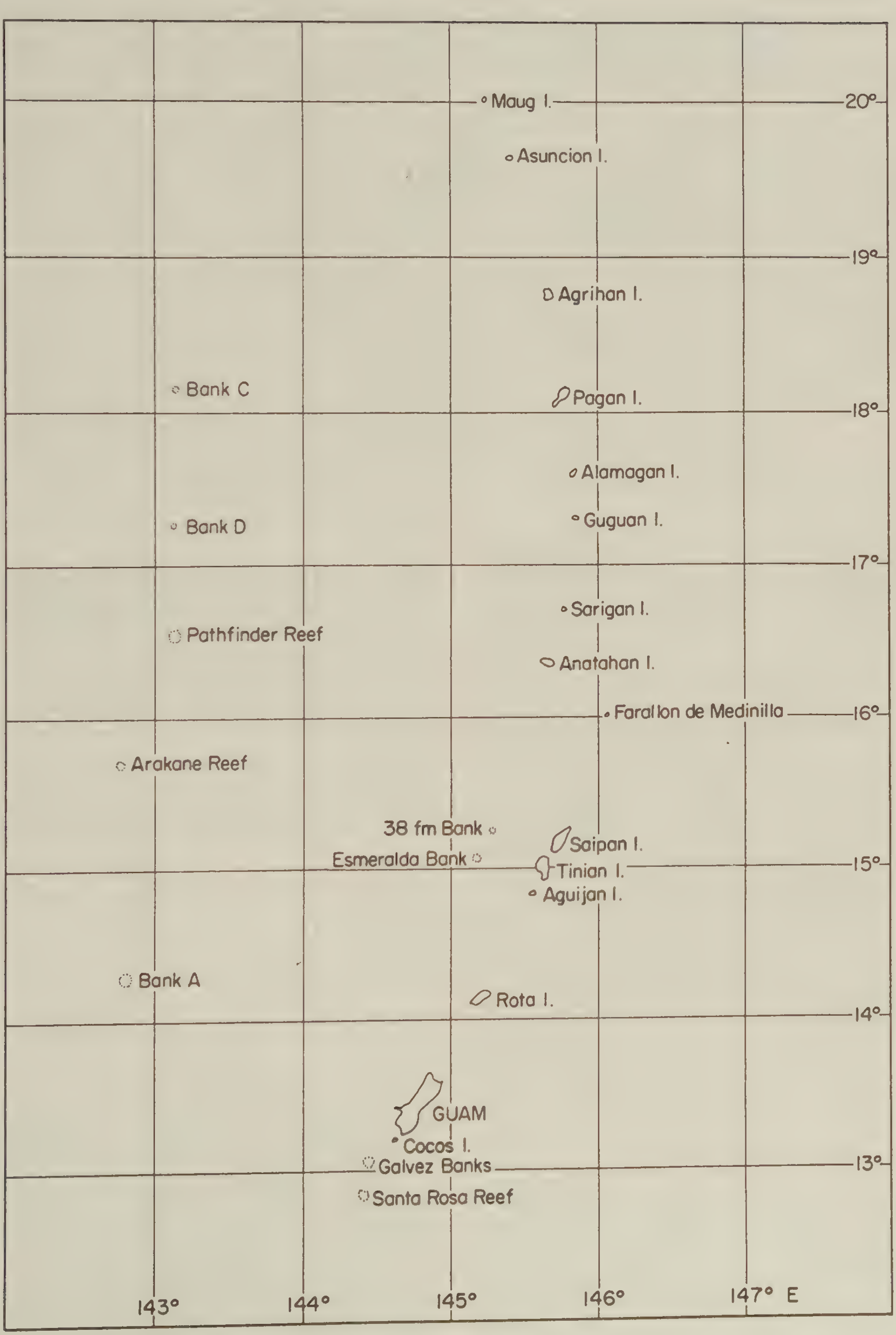
[2] Moffitt, R. B., and J. J. Polovina. In prep. Distribution and yield of the deepwater shrimp resource in the Marianas. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.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Farallon de Medinilla
Arakane Reef
38 fm Bank
Saipan I.
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FIGURE 1.—Map of the Mariana Archipelago.

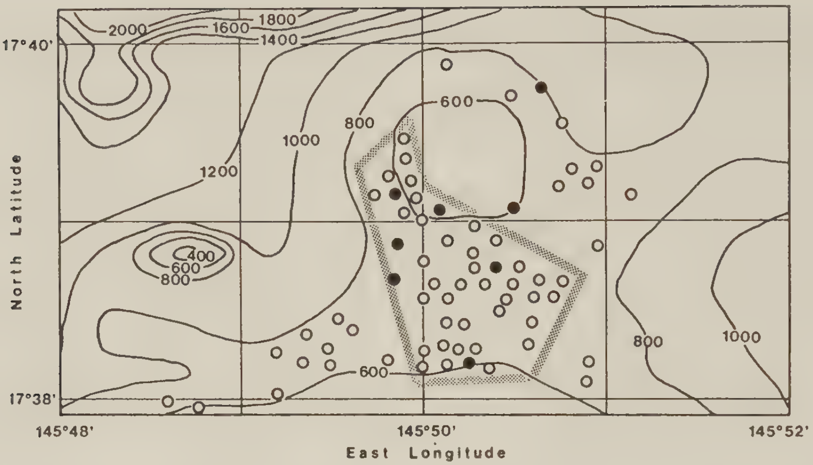

FIGURE 2.—Contour map of the Alamagan study site. Isobaths given in meters. Open circles represent set locations of standard traps (one set is composed of five traps); closed circles show sets of the pyramid trap. The stipple border encloses the area of greatest fishing intensity. One minute latitude = 1.85 km.

concentrated in the area enclosed by stipple borders, where 65% of all sets (44 of 68) occurred. This area represents 312 horizontal ha of shrimp habitat.

TABLE 1.—Summary of catch and effort statistics of the intensive fishing experiment for *Heterocarpus laevigatus* at Alamagan Island, 9-24 January 1984. All catches in kilograms and effort in standard trap-nights. CPUE includes only standard trap catches.

Date (mo/d/yr)	Standard trap catch	Pyramid trap catch	Corrected cumulative catch	Daily effort	CPUE
1/9/84	62.52	—	31	20	3.13
1/10/84	42.30	37.65	102	18	2.35
1/11/84	64.61	—	175	20	3.23
1/12/84	44.96	23.86	241	17	2.64
1/13/84	85.80	6.72	322	20	4.29
1/14/84	42.90	22.98	401	19	2.26
1/15/34	47.79	—	458	15	3.19
1/16/84	34.27	6.60	503	14	2.45
1/17/84	34.57	3.18	542	19	1.82
1/18/84	34.57	2.41	579	20	1.73
1/19/84	39.01	9.37	622	20	1.95
1/20/84	41.23	—	667	20	2.06
1/21/84	27.10	—	701	20	1.36
1/22/84	28.75	—	729	14	2.05
1/23/84	32.98	—	760	15	2.20
Total	663.36	112.77		271	

Intensive Fishing Experiment

Although 20 standard shrimp traps were set daily for 15 consecutive days, 29 traps were lost due to entanglement on the bottom. This resulted in 271 effective trap-nights of standard fishing effort and a gear loss rate of 9.7% (Table 1). The loss of shrimp traps is not believed to have affected the outcome of the intensive fishing experiment for two reasons: First, the Pacific mackerel bait was rapidly exhausted in the traps, as evidenced by its condition after a single night's soak; second, large holes were usually evident in traps if the fishing gear was successfully retrieved after being fouled on the bottom.

The catch of *H. laevigatus* was quite pure; only trace amounts of *H. longirostris*, *H. ensifer*, and the eel *Synaphobranchus affinis* co-occurred in the traps. The latter species was observed to consume individual *H. laevigatus* on occasion, but this had a negligible impact on overall catch rates of the shrimp.

A total catch of 663.36 kg of *H. laevigatus* was landed from standard traps, yielding an overall CPUE of 2.45 kg/trap-night (Table 1). In addition, another 112.77 kg were taken in eight sets of the pyramid trap for an overall CPUE of 14.10 kg/trap-night (Table 1). The larger commercial trap outperformed individual standard Honolulu Laboratory traps by a ratio of 5.76 to 1. Thus, one set of the large trap was roughly equivalent to one set of a string of five standard traps, but the former was much more variable in its performance. Overall, a total of 776.13 kg of *H. laevigatus* were removed from the study area during the 16-d experiment. These averaged 28 g each (16 shrimp/lb).

The data presented in Table 1 are arranged to be fitted by the Leslie model (Ricker 1975). The CPUE was computed each day based solely on standard trap catch and effort statistics, although cumulative removals included catches from the large commercial trap. As in Ricker (1975), CPUE is regressed against corrected cumulative catch, defined as the cumulative catch prior to the start of an interval plus half the catch taken during the interval (see also von Geldern 1961).

Standard daily CPUE is plotted against cumulative catch removed in Figure 3. The slope of the regression is significantly less than zero (one-tailed test, $t = -2.80$, df = 13, $P = 0.01$). Estimates of slope, intercept, and mean squared error were -0.001945 trap-night^{-1}, 3.334 kg/trap-night, and 0.3754 (kg/trap-night)^2, respectively. Consequently, the catchability coefficient is estimated to be $\hat{q} = 0.001945$ trap-night^{-1} and the initial population size prior to the start of fishing to be $\hat{n} = 1{,}714$ kg. Confidence intervals for these estimates are $P(0.0004 < q < 0.0034) = 0.95$ and $P(1150 < n < 6005) = 0.95$ (Ricker 1975). Notice that the confidence interval for the estimate of initial population biomass (n) is asymmetrical about the point estimate.

Crittenden (1983) and others have warned against unequal variance in plots of CPUE against cumulative catch. To test for this possibility, the absolute values of the residuals from Figure 3 were ranked and the corrected cumulative catches were ranked. A Spearman rank correlation coefficient was then calculated, resulting in $r_s = -0.189$, $P = 0.50$. From this analysis there is no evidence of heteroscedasticity. Further, there is little to suggest curvilinearity in Figure 3. A runs test (Tate and Clelland 1957) on the signs of the residuals indicates they are randomly sequenced ($P > 0.40$). This result supports the assumption of constant catchability.

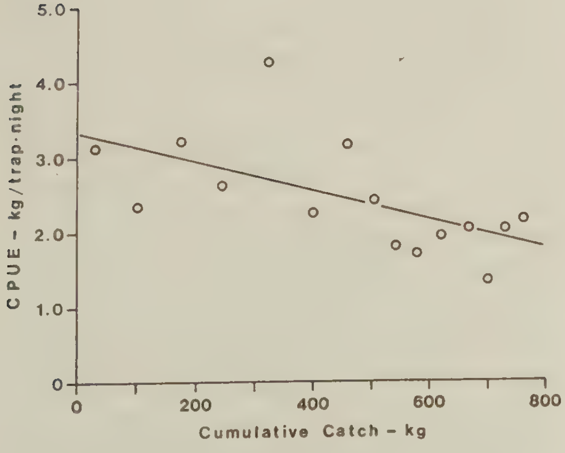

FIGURE 3.—Leslie model applied to *Heterocarpus laevigatus* at Alamagan. Each point represents 1 day of fishing. Data from Table 1.

At the time the experiment was terminated, 776 kg of shrimp had been removed by trapping. An estimate of the concomitant catch rate can be calculated from the regression equation of Figure 3. This estimate of CPUE is 1.82 kg/trap-night. When the *Townsend Cromwell* returned to the study site, 4 mo later, the mean catch rate was 1.91 kg/trap-night (42 effective standard trap-nights of effort, $s = 1.33$), this based on a total catch of 80.08 kg *H. laevigatus*. The preceding calculations include only those traps which were baited comparably to the experimental traps (three chopped Pacific mackerel). Traps with two whole baits ($n = 42$) yielded an average catch rate of 1.39 kg/trap-night ($s = 1.09$).

Length-Frequency Distributions

Examination of size-composition data can help interpret changes in weight CPUE. Declining trap catch rates could, for example, represent fewer individuals of the same size. Conversely, a decline in the average size of individuals caught with no change in numbers would also result in declining CPUE.

The three length-frequency distributions of *H. laevigatus* sampled during the period of experimental fishing are presented in Figure 4. For each distribution the date of capture, depth of capture, sample size, and mean carapace length are provided. Although appearing superficially similar, the results of ANOVA show that significant differences exist in size composition among the three samples ($F = 10.03$, df = 2, 343, $P < 0.001$). These differences, however, do not explain the decline in CPUE. The data in the figure show that the mean size of *H. laevigatus* actually increased over time, and that the overall decline in CPUE observed in Figure 2 must therefore have been due to a decrease in the number of shrimps caught.

DISCUSSION

Powell (1979) has shown that the shape of the descending limb of length-frequency distributions can provide useful information concerning the relationship between mortality and growth. Specifically, the ratio of Z (instantaneous total mortality rate) to K (von Bertalanffy growth coefficient) is defined in a simple way by the interrelationship of the least size when fully vulnerable to the gear, the mean size in the catch of fully recruited individuals, and the

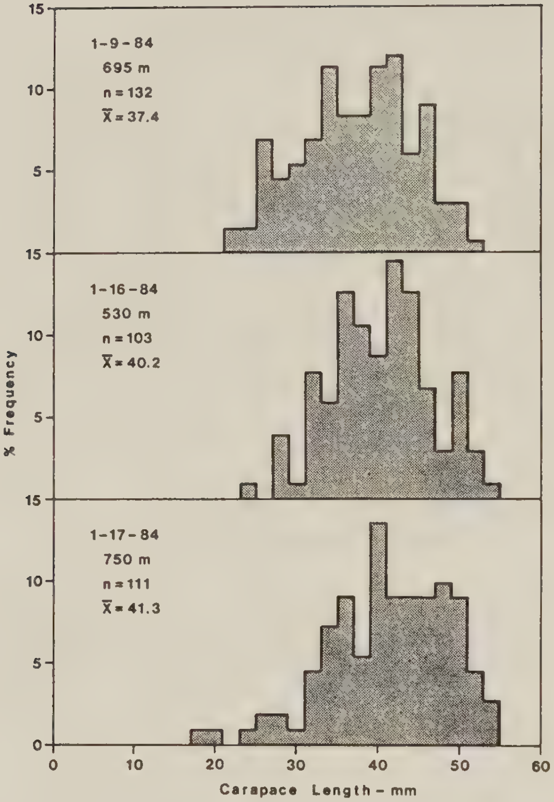

FIGURE 4.—Length-frequency distributions of *Heterocarpus laevigatus* taken in shrimp traps.

von Bertalanffy asymptotic size (L_∞). This is true if the following conditions hold: 1) the growth of individuals follows a deterministic von Bertalanffy growth curve, 2) mortality is constant and uniform for all ages, and 3) recruitment is constant and continuous over time (Beverton and Holt 1956).

Results presented in Dailey and Ralston (1986) provide the basis for estimating the minimum CL when *H. laevigatus* becomes fully recruited to the trap fishery. They provide a regression equation relating carapace width (CW) to CL. In this study the smallest mesh dimension of standard shrimp traps was 1.27 cm. This provides a logical cutoff point for measurement of least CW for shrimp that are fully vulnerable to the gear. Based on their functional regression this corresponds to 30 mm CL.

It is evident from the three panels in Figure 4 that the size distribution of *H. laevigatus* above 30 mm CL is characterized by both rising and descending portions. As shown by Powell (1979) this indicates a Z/K ratio of less than unity (i.e., instantaneous mortality rate is less than the growth coefficient). Alternatively, it is possible that the rising portions of the length distributions are not representative of the population sampled, but are instead a reflection of behavioral interactions among shrimp of different sizes. Chittleborough (1974), for example, has shown that the presence of large individuals of the decapod crustacean *Panulirus cygnus* inhibited smaller conspecifics from entering baited traps, even though smaller lobsters were vulnerable to the traps in the absence of large ones. If this kind of behavioral interaction was also in evidence here, the effective least size of *H. laevigatus* when fully vulnerable to the traps may be as large as 41 mm CL, the mode of the pooled length-frequency distribution. This would indicate a Z/K ratio of 2.0 because of the linearity of the descending portions of the size-frequency distributions. Only further experimentation will resolve this issue.

With respect to the intensive fishing experiment it is useful to consider whether or not the basic assumptions of the Leslie model were violated during the course of the study. The first of these was closure of the population. Two factors support the contention that the study population was effectively isolated and that the effects of immigration and emigration were negligible. First, the hydrographic survey showed that the study site comprised a semi-isolated extension of the main island. Continuity of prime habitat (600-800 m depth) with the island proper extended along two narrow corridors to the southeast and southwest. The shrimp has been taken as shallow as 400 m and as deep as 950 m in the Mariana Archipelago, but the 600-800 m depth range encompasses the preponderance of the region's shrimp stock (Moffitt and Polovina fn. 2), although elsewhere (e.g., Fiji, Vanuatu, and Samoa) the depth distribution apparently extends into somewhat shallower water (King 1984). The second factor arguing for closure is that the catch rate of *H. laevigatus* remained low after a 4-mo hiatus in fishing. If movements or migrations of shrimp were biologically significant over this time interval, a larger change in CPUE would be expected. It is tempting to attribute the small increase in catch rate (4.9%) to some type of biological recovery, but the estimate of mean squared error in CPUE from Figure 3 (0.3754 kg^2/trap-night^2) indicates that background variation is too large for the observed difference to be significant. Regardless, the data support the assumption that the population is closed.

The second assumption was that growth, natural mortality, and recruitment are negligible factors in accounting for changes in CPUE. That the experiment was completed in only 16 d and the population was reduced an estimated 45.3% are persuasive elements here. Additionally, the size-frequency data show no indication of a major alteration in population structure. As long as the selective properties of the fishing gear remain unchanged, alterations in the length composition of the catch are not expected over short time intervals, at least due to the direct effects of fishing. Further, no recruitment of small shrimp is evident. That the mean size of *H. laevigatus* seemed to increase as the experiment progressed might support the hypothesis that growth of the stock was significant. An alternate explanation, however, is that size structure varies with depth of capture. Results from the Hawaiian Islands (Gooding 1984; Dailey and Ralston 1986) have now demonstrated this. The three samples presented in Figure 4 are confounded by this variable; other unknown factors may also have affected the shrimp size-frequency data (e.g., sexual dimorphism, contagious dispersion, sampling error, etc.). In addition, the estimated growth rate from the data (3.9 mm CL over 8 d = 0.49 mm/d) is biologically untenable.

Other investigators, notably Schnute (1983) and Crittenden (1983), have cautioned against the effects of changing catchability and unequal variance on Leslie model estimates. From the data gathered, there is little statistical evidence to suggest that these factors affected parameter estimates and I therefore assume that 0.001945 trap-night^{-1} and 1,714 kg are reasonable estimates of standard trap catchability and virgin population size, respectively.

Given that the virgin biomass of *H. laevigatus* in the study area was 1,714 kg, the next question is: How large an area was intensively fished? From Figure 2 it is clear that there is no simple answer to this question. A number of sets were located in areas peripheral to the main trapping area. Designating the stipple bordered area as the effective area fished is arbitrary, but provides a useful starting point to allow calculation of shrimp densities. This area was calculated to be 312 ha, corresponding to a projected density of 5.5 kg of exploitable *H. laevigatus* per hectare. Since individuals weighed 28 g each, on average, this is equivalent to 1 exploitable shrimp/51 m^2 of bottom, a remarkably low density. Furthermore, a catchability coefficient of 0.001945 trap-night^{-1} indicates that one unit of standard trap effort can reduce a 312-ha population of shrimp by about 0.2%. This is certainly a significant impact. The vulnerability to trapping that this species demonstrates is cause for attention and careful resource management.

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AN ECOLOGICAL SURVEY AND COMPARISON OF BOTTOM FISH RESOURCE ASSESSMENTS (SUBMERSIBLE VERSUS HANDLINE FISHING) AT JOHNSTON ATOLL

STEPHEN RALSTON,[1] REGINALD M. GOODING,[1] AND GERALD M. LUDWIG[2]

ABSTRACT

The deep slope (100-365 m) environment at Johnson Atoll in the central Pacific was surveyed with a submersible and the standing crop of commercially important bottom fishes (i.e., lutjanids, serranids, and carangids) estimated by visual quadrat censusing. Results are compared with an assessment made by hook-and-line fishing.

Overall, 69 species of fish were recorded from the submersible and 10 from fishing. Well over half of the sightings from the submersible were new locality records. Bottom fish abundance estimates (fish/hectare and fish/line-hour) varied by site but agreed broadly with one another. Together they are used to estimate catchability (0.0215 hectare/line-hour), which is shown to vary through the day.

Bottom fish were contagiously dispersed along both vertical and horizontal dimensions, with increased numbers of the snapper *Pristipomoides filamentosus* in upcurrent localities. On a finer scale this species and *Etelis coruscans* were aggregated near underwater promontories and headlands, but at different depths.

Numerous observations concerning the deep slope environment of this central Pacific Ocean atoll are included.

Perhaps the most widespread precept in fisheries today is the supposition that catch rate is proportional to stock abundance (Gulland 1974; Ricker 1975; Pitcher and Hart 1982). Even so, there are numerous studies which demonstrate exceptions to this assumption (see for example MacCall 1976; Bannerot and Austin 1983). A departure from linearity in the relationship of these two variables reflects varying catchability. This variation may be due to schooling behavior, gear saturation, or any number of other factors which affect catch per unit effort (CPUE) in addition to stock abundance (Rothschild 1977). It is often difficult, if not impossible, to evaluate the validity of the linearity assumption in most practical situations. A multiple approach to stock assessment has often been suggested as a means of circumventing this problem, including the use of hydroacoustics (Barans and Holliday 1983; Thorne 1983), underwater television-diver surveys (Powles and Barans 1980), and submersibles (Uzmann et al. 1977) to corroborate CPUE data. Consistency in results among a set of independent assessment techniques is necessary for validation and verification of data.

Submersibles in particular have also proven useful in studying the distribution of fishes in various deepwater habitats (Brock and Chamberlain 1968; Strasburg et al. 1968; Colin 1974; Shipp and Hopkins 1978), in identifying nursery grounds of commercially important rockfish species (Carlson and Straty 1981), and in assessing the effectiveness of baited longline gear (High 1980; Grimes et al. 1982). In many situations submersibles provide an ideal means of independent assessment (Uzmann et al. 1977) if questions concerning bias in visual surveys can be adequately addressed (Colton and Alevizon 1981; Sale and Douglas 1981; Brock 1982).

The purpose of this study was to examine the distribution and abundance of tropical deep slope bottom fishes (i.e., lutjanids, serranids, and carangids) at Johnston Atoll in the central Pacific Ocean with a research submersible and to compare the results with an assessment made by fishing. This comparison provides not only a basis for testing the validity of a CPUE statistic, but also for estimating the catchability coefficient. Both are important issues because of the widespread use of hook-and-line catch and effort statistics in resource assessments of bottom fish stocks worldwide (Moffitt 1980; Ralston 1980; Ivo and Hanson 1982; Ralston and Polovina 1982; Munro 1983; Forster 1984). Of special interest was determining the relationship between CPUE and visual estimates of bottom fish standing stock.

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[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

[2] U.S. Fish and Wildlife Service, Honolulu, HI 96850; present address: Florida Fishery Research Station, U.S. Fish and Wildlife Service, P.O. Box 1669, Homestead, FL 33030.

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In addition, a variety of observations made from the submersible substantially improved our understanding of factors controlling the distribution and abundance of the entire deep slope fauna at Johnston Atoll.

DESCRIPTION OF THE STUDY AREA

A National Wildlife Refuge since 1926, Johnston Atoll is located 1,250 km southwest of Oahu, HI. The atoll's physical environment has been reviewed by Amerson and Shelton (1976) and is summarized here.

Located between lat. 16°40′-16°47′N and long. 169°24′-169°34′W (Fig. 1), Johnston Atoll lies in the North Pacific central water mass, where salinities range from 34.8 to 35.3‰. Surface water temperatures show little seasonality, ranging from 25° to 27°C. The atoll is directly in the path of the westerly flowing North Equatorial Current, with surface currents typically 0.5 kn (0.25 m/s). Deeper layers flow smoothly past the atoll, but an island wake forms in lee surface waters, with effects evident up to 600 km downstream (Barkley 1972).

The atoll is composed of a coral platform, encompassing over 130 km^2 of reef under water <30 m deep. A narrow lagoon lies between the northwest barrier reef and Johnston and Sand Islands to the southeast (Fig. 1). The atoll is unusual in that the main outer reef extends only about one quarter of the way around its perimeter (Fig. 1). A large portion of the atoll lies exposed to prevailing easterly weather conditions without benefit of barrier reef protection. Evidence suggests that subsidence and tilting of the reef platform to the southeast created this unusual condition.

The climate is tropical marine, i.e., there is little seasonal variation in temperature and windspeed, but substantial variation in rainfall. A 4-mo "winter" season extends from December to March, when temperatures drop slightly, winds become more variable, and precipitation increases. The mean annual air temperature is 26.3°C, with a daily range of 4.0°-4.5°C. Daily maximum and minimum temper-

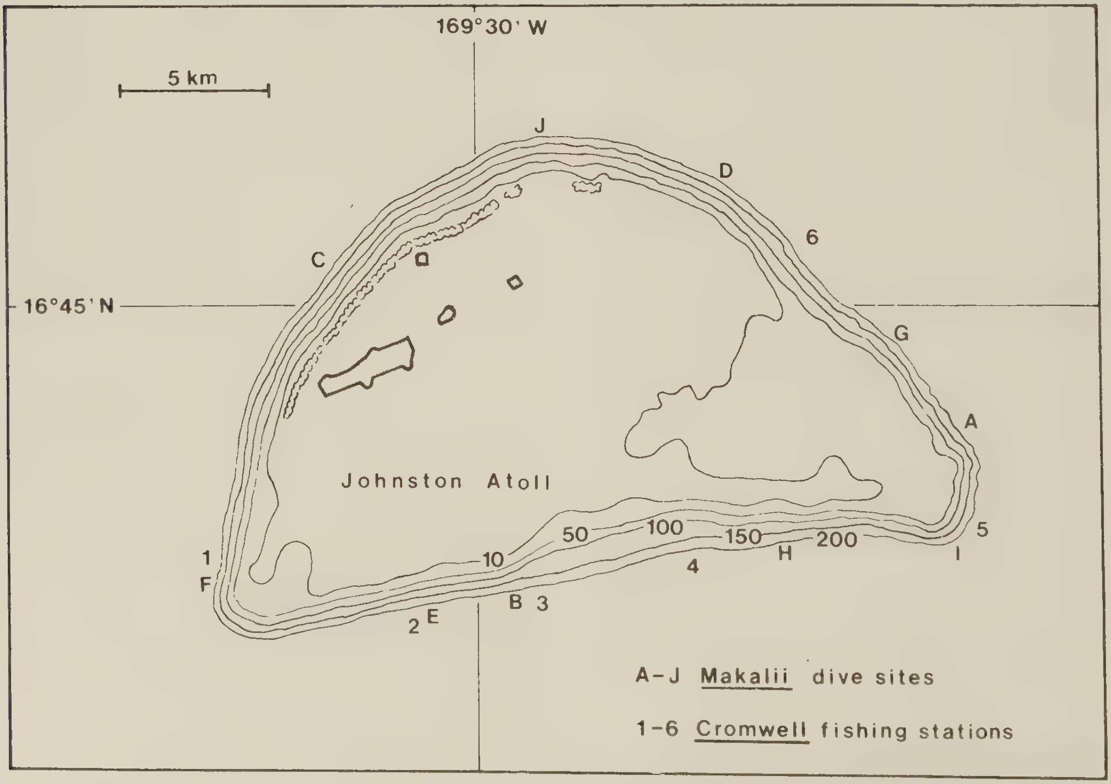

FIGURE 1.—Map of Johnston Atoll. The lines encircling the atoll are isobaths of constant depth (fathoms). The four shaded areas at the upper left are emergent lands (Johnston, Akau, Hikina, and Sand Islands). Letters (A-J) indicate the 10 dive sites of the *Makalii* during the study. Numbers (1-6) indicate fishing stations of the *Townsend Cromwell*.

atures vary little throughout the year, as do sea surface temperatures, which are in near equilibrium with the air. Strong easterly trade winds prevail all year but increase during the summer period. Annual mean wind speed at Johnston Island is 13 kn (7.5 m/s) and monthly means range from 11 to 14 kn (5.5-7.0 m/s).

METHODS

Makalii

The *Makalii* is operated by the National Undersea Research Laboratory at the University of Hawaii. It is a two-man, battery powered, 1-atmosphere submersible which is 4.8 m long, with a pressurized capsule 1.5 m in diameter. When carrying a pilot and one observer, its normal operating speeds range from 1 to 3 kn (0.5-1.5 m/s). Maximum dive duration is 4-5 h and depth capability is 365 m. Equipment carried in this study included hydraulic manipulator, internal and external color video cameras, 2 video monitors, video recorder, video flood lights, Photosea[3] 35 mm still camera with strobe, current and temperature meters, and a dictaphone tape recorder. In addition, the *Makalii* is equipped with an environmental monitoring system for continuous recording of temperature, salinity, conductivity, oxygen, solar radiation, and depth.

All three authors participated as observers during a series of dives at Johnston Atoll over the 2-wk period between 22 September and 5 October 1983. Once on station, a launch-recovery-transport platform was submerged to 20 m and divers released the *Makalii*, usually in 120 m of water. The submersible descended until encountering the bottom and locating the atoll's shelf break. Observations made on fishes during the dives were voice and video recorded for later analysis. Slope angle was periodically measured with a hand-held inclinometer.

Visual estimates of the density of commercially important bottom fishes (sensu Ralston and Polovina 1982) were made by a series of "quadrat" samples. These fishes included *Cookeolus boops*, *Epinephelus quernus*, *Aphareus furcatus*, *A. rutilans*, *Etelis carbunculus*, *E. coruscans*, *Pristipomoides auricilla*, *P. filamentosus*, *P. zonatus*, *Carangoides orthogrammus*, *Caranx lugubris*, *Seriola dumerili*, and *Pontinus macrocephalus*.

During quadrat sampling the observer would look out his port and count the total number of bottom fish, without regard to species, over an area of the bottom judged to be 30 m^2. Quadrat areas always lay on the oblique planar surface of the slope face and were away from the immediate vicinity of the submersible. A sampling period consisted of four counts systematically performed, one every 15 s. To the extent possible, each count was made at an instant in time. All bottom fish seen in the water column above the sample area were included in counts.

The submersible progressed stepwise down the slope (100-365 m) in a clockwise direction around the atoll, with the observer's starboard port always oriented to the slope face. Upon reaching the *Makalii*'s depth limit, a slow stepwise ascent would begin to 100 m, where the dive would end. Descents generally lasted 2.5 h and ascents 1.5 h. Thus the entire vertical distribution of the deep slope was sampled more or less equally (i.e., observations were not concentrated in any particular depth zone).

Townsend Cromwell

The National Oceanic and Atmospheric Administration's (NOAA) RV *Townsend Cromwell* is 50 m long and when rigged for bottom handline fishing carries four hydraulic fishing gurdies (Charlin motors and Pacific King fishing reels), each with 365 m of braided prestretched 90 kg Dacron line. The terminal rig is composed of four No. 28 Tonkichi round fishing hooks and a 2 kg weight. Stripped squid was used for bait and fishing was conducted only during the day.

The vessel spent 3 d (3-5 November 1983) at Johnston Atoll sampling deep slope bottom fish by drift fishing. After wind and current directions had been determined, the vessel was positioned over the desired depth and fishing lines were dropped. Fishing continued until the vessel drifted over an unsuitable water depth, when lines were retrieved and the *Townsend Cromwell* repositioned. Single drifts were the fundamental sampling unit by which catch and effort statistics were summarized. Six fishing stations were occupied (Fig. 1), one during the morning and afternoon of each day. Fork length to the nearest millimeter and depth of capture were recorded for all fish landed.

RESULTS

Makalii

Ten dives were completed at Johnston Atoll (Fig. 1). Due to precipitous dropoffs which occur throughout the study area (100-365 m), the length of the atoll's 183 m (100 fathom) isobath (64 km) provides a convenient measure of total deep slope habitat (Ralston and Polovina 1982). The average point-to-point distance covered by the submersible during one 4-h dive was 2.27 km (s = 0.56 km). An aggregate 22.7 km were thus surveyed during this study, comprising 35% of the deep slope habitat at the atoll.

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Temperature

Ambient temperature and depth were recorded often during dives, from which temperature-depth profiles were later constructed. The results are summarized in Figure 2. The solid line represents median temperatures at depth, with the shaded area encompassing the range of temperatures observed among all 10 dives. Surface water temperature was typically 27°C and the mixed layer 100 m deep. A second weak thermocline was found around 240 m. Although its depth varied somewhat (220-245 m), it was present around the entire atoll, i.e., both windward and leeward exposures, and was observed as a shimmering layer below the submersible as it descended. This effect is believed due to refraction of light passing through variable density water, a result of the thermocline in association with a decrease in salinity.[4] Ambient water temperature usually had dropped to 8.5°C at a depth of 350 m.

Slope Angle

The relationship between the bottom's slope and depth was also measured. These data were summarized after each dive and bottom contours plotted. Overall, there was little variation in slope angle around the atoll, i.e., the general pattern was one of uniformity at all sites visited. Figure 3 presents pooled results for all slope angle-depth determinations. In the figure, horizontal and vertical scales are equal and the composite contour of the bottom (100-365 m) at Johnston Atoll is shown in profile. The slope was stratified into three 50-fathom depth zones for later analysis.[5] The slope angle between 50 and 100 fathoms averages Θ_1 = 25° (Table 1). Similarly, Θ_2 = 47° and Θ_3 = 59°. There is a definite trend at Johnston Atoll for the slope to steepen with increasing depth, at least between 100 and 365 m.

In the shallowest regions surveyed (<125 m) the bottom was a monotonous sandy plain in the shoreward direction, but at 125 m it began to slope steeply

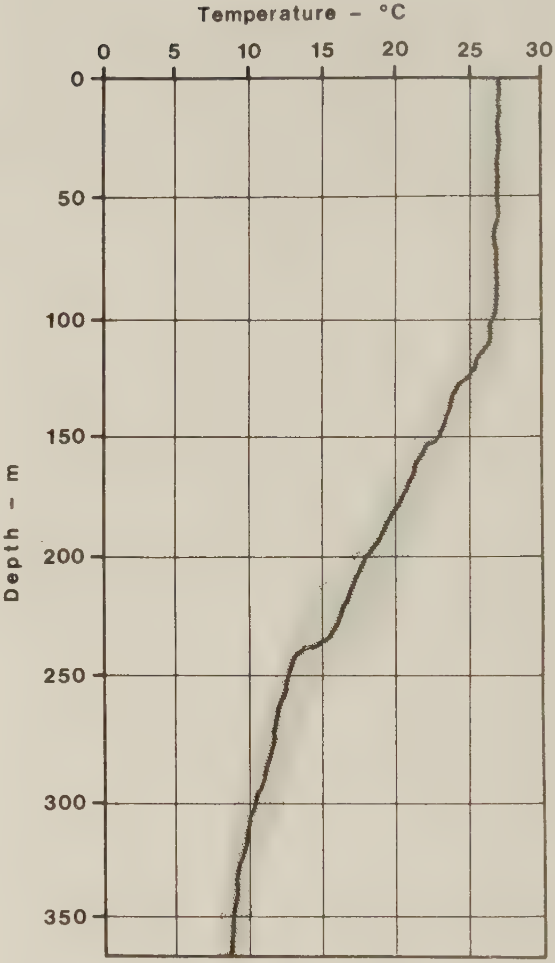

FIGURE 2.—The pooled relationship (n = 10) between temperature and water depth at Johnston Atoll. Solid line = median values; shaded area = range of values.

TABLE 1.—Total habitat areas stratified by depth zones at Johnston Atoll.

Depth stratum (fathoms)	Digitized horizontal planar areas (ha)	Slope angle	Oblique planar habitat areas (ha)
Emergent lands	305 (1%)	—	—
0-10	15,012 (60%)	—	—
10-50	6,123 (24%)	—	—
50-100	1,624 (7%)	25°	1,785
100-150	964 (4%)	47°	1,418
150-200	1,020 (4%)	59°	1,962
Total	25,048 (100%)	—	5,165

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[4] E. Chave, Hawaii Undersea Research Laboratory, University of Hawaii, Honolulu, HI 96822, pers. commun. June 1984.

[5] Stratification of depth into zones was performed using units of fathoms (1 fathom = 1.83 m) because nautical charts, hydrographic surveys, and fathometers are so measured. For the sake of brevity and clarity, isobaths and depth strata will henceforth be given only in this unit of measure.

downward. Although not easily seen in the figure, a small but prominant ledge 5-10 m high encircled the atoll between 130 and 140 m. Somewhat deeper, between 180 and 275 m, the bottom was uniform in slope and its surface relatively smooth and devoid of features. Slope angles approached the vertical at most sites in the 300-350 m depth range, with overhanging caves formed by subaerial dissolution.[6] At the deepest points visited (360 m) the bottom became less precipitous, and in some areas a sediment-laden terrace had formed along the base of the deep dropoff.

Based on estimates of slope angle, existing charts, and a hydrographic survey by the *Townsend Cromwell*, habitat areas for the three depth zones were determined. The positions of the 10 and 100-fathom isobaths were already known, but they were refined and the locations of the 50-, 150-, and 200-fathom isobaths estimated. Figure 1 is a simplified representation of a much larger chart which was digitally analyzed to determine the horizontal (i.e., level) areas bounded by isobaths (Table 1). The results show that emergent lands (Johnston, Akau, Hikina, and Sand Islands) account for only 1% (305 ha) of the level planar area of the atoll. The largest area (60%) lies between sea level and 10 fathoms. The total horizontal extent of the atoll is about 25,000 ha.

These results can be misleading, however, because a vertical slope provides no horizontal habitat area, and yet both reef fish diversity and standing crop are known to be positively correlated with topographic relief (Luckhurst and Luckhurst 1978; Gladfelter et al. 1980; Carpenter et al. 1981). At Johnston Atoll the structural complexity of the substratum frequently increased with slope angle. A better estimate of total habitat is the area of bottom irrespective of slope angle, estimated by dividing the horizontal planar area of a depth stratum by the cosine of the slope angle within it. This adjustment almost doubles the estimate of total habitat area in the 150-200 fathom zone, simply due to the precipitous dropoff found there. A composite 5,165 ha of habitat occurs between 50 and 200 fathoms.

General Observations

While this study focused primarily on the deepwater ichthyofauna of Johnston Atoll, many observations were made on the oceanographic, geologic, and biotic characteristics of the study area. These are briefly recounted here.

Currents running in directions parallel to the slope were frequently encountered. They were generally weak and did not exceed 0.3 kn (0.15 m/s). They sometimes exhibited reversals with depth. During

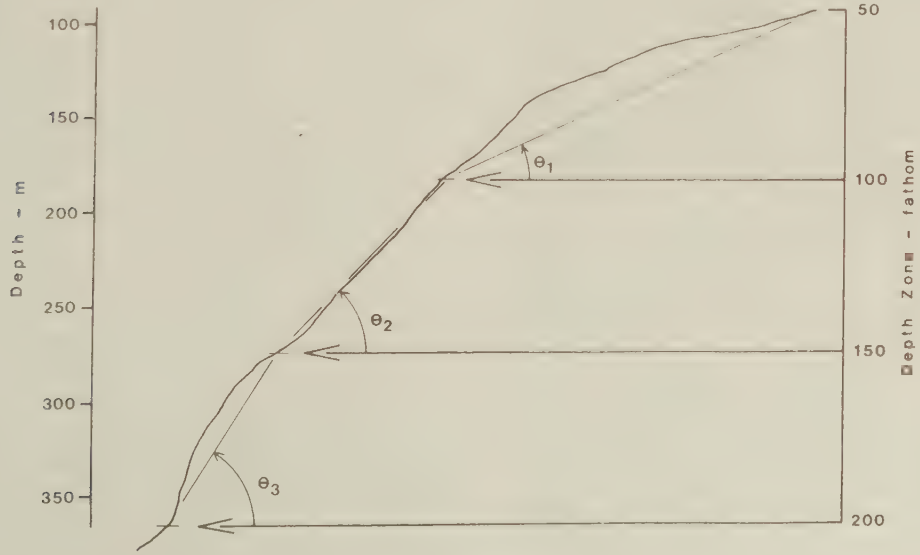

FIGURE 3.—Composite reconstruction of the deep slope at Johnston Atoll. Horizontal and vertical scales equal. Average slope angles (Θ) were measured for each of three 50-fathom depth strata.

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[6] Keating, B. H. Geologic history and evolution of Johnston Island: Submersible dive results. Manuscr. in prep. University of Hawaii, Honolulu, HI 96822.

dive F, for example (Fig. 1), a 0.2 kn (0.10 m/s) current was observed at 125 m running south (i.e., counterclockwise when viewed from above). There was no current between 180 and 275 m. At 300 m, however, a 0.1 kn (0.05 m/s) current was observed, traveling in a northerly direction (i.e., clockwise). A similar depth-related current reversal was observed during dive C, although on this occasion the shallower current (170 m) ran clockwise and the deeper one (290 m) counterclockwise. In contrast, a weak downslope current (0.1 kn or 0.05 m/s) was observed but once (dive E at 305 m). No upwelling currents were encountered.

Geologically, the deep slope of Johnston Atoll was grossly similar at all points visited. The low escarpment at 130 m was most likely due to erosion of an ancient limestone reef. This feature was characterized by mounds of coral rubble, boulders, small undercut caves, and a profusion of fishes. Below it the slope angle was remarkably uniform, with low topographic relief. The bottom was still composed of limestone and showed severe biological and chemical weathering (i.e., dissolution) along the slope gradient, being pitted and striated with numerous shallow depressions. Few sediments or boulders were observed. At a depth of 240 m topographic relief increased, as large slab boulders became increasingly prominent. Subaerial dissolution had produced low shallow limestone caves, and fine sediments were more common. Between 290 and 335 m the slope was very steep, with a well-developed system of sharp ridges and deep erosional channels. The substratum had the superficial appearance of dark basalt but was composed of thin manganese crusts overlying ancient limestone reef materials (Keating see footnote 6). Fine sediments spilled down the channels in the slope and piled up at the base of the deep dropoff (350 m). More limestone boulders were arrayed along this deep terrace and fine sediments covered the bottom.

As expected, few fleshy macroalgae were seen. The only algae encountered regularly were two corallines, *Halimeda* sp. and an unidentified crustose species. The former occurred in small scattered clumps between 100 and 200 m, with loose remnant exoskeletal "sands" found in sediment pockets as deep as 290 m. The crustose form was abundant between 150 and 250 m where it covered much of the slope face. Otherwise, an unidentified species of brown algae seen on dive H between 150 and 250 m was the only other algae seen. A more detailed description of the algal biota at Johnston Atoll is in preparation.[7]

In contrast to the depauperate flora, the invertebrate fauna was rich. Listed here are those forms seen often enough to constitute indicator species for particular depth strata. In addition to these a great many others were observed and photographed. In the Cnidaria, three stoney corals were especially plentiful: *Leptoseris hawaiiensis* (115-165 m), *Stylaster* sp. (135-245 m), and *Madracis* sp. (140-200 m). Several species of black corals (Order Antipatharia) were also common. Of the crustaceans, a single large *Panulirus marginatus*, previously known only from one specimen (Brock 1973), was observed in a small hole during dive A at 122 m, and at least two types of galatheid crab were very abundant in small holes pitting the reef slope between 230 and 350 m. In deep water the remaining attached valves of dead rock oysters were seen in patches along the base of the deep dropoff (350 m), as was an unidentified species of solitary tunicate (335-365 m). Echinoids were particularly abundant immediately below the shelf break; e.g., *Diadema* cf. *savignyi* (110-170 m), *Chondrocidaris gigantea* (120-160 m), and heart urchins (Brissidae, 130-200 m). Other than galatheid crabs, the 220-310 m zone was largely barren and devoid of megabenthos.

Ichthyofauna

A total of 69 fish species in 29 families were observed during *Makalii* dives (Table 2). Overall, the proportional representation of different families was similar to that of the shallow water community (Gosline 1955; Randall et al. in press), although the representation of genera was grossly different. Serranid species were most numerous with nine species observed (eight in the anthiine subfamily). Lutjanids were also abundant (eight species), but no members of the ubiquitous genus *Lutjanus* were seen. Forty of the species listed in Table 2 (58%) are new records for Johnston Atoll (Randall et al. in press). Photographs of several fishes observed during dives are presented in Figure 4.

An indication of species' depth distributions is given in Table 2. Because no observations were made in <100 m, upper limits can be misleading. This is particularly true of shallow-water species which penetrated to the 135 m escarpment but not beyond, including: *Triaenodon obesus*, *Parapercis schauinslandi*, *Aphareus furcatus*, *Chromis verater*, *Parupeneus cyclostomus*, *P. multifasciatus*, *Forcipiger flavissimus*, *Holacanthus arcuatus*, *Bodianus bilu-*

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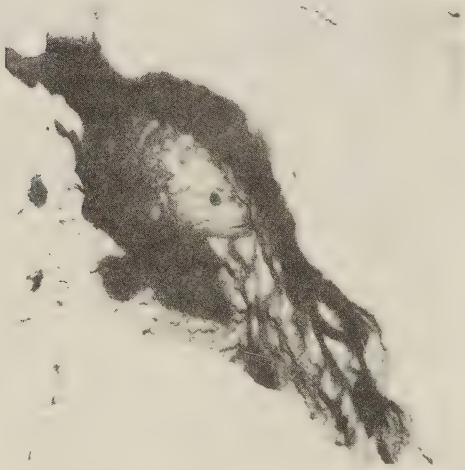
[7] C. Agegian, University of Hawaii, Honolulu, HI 96822, pers. commun. June 1984.

TABLE 2.—Fishes encountered during dives (100-365 m) of the *Makalii* at Johnston Atoll. Included for each species are the minimum and maximum depths (m) of observation as well as the median and range of the depth distribution. Under the sighting column a value of 1 indicates a species was seen repeatedly (>5 times) during each dive of the submersible, 2 means the species was occasionally seen on each dive (<5 times), 3 signifies sightings on most dives but not all (i.e., species seen on several occasions), and 4 indicates rarity (see only once or twice during all dives). An asterisk to the left of a species name signifies a new record for Johnston Atoll (Randall et al. in press).

Family-species	Min-max	Median (range)	Sighting
Carcharhinidae			
Carcharhinus amblyrhynchos	90-275	185(185)	1
Carcharhinus sp. (probably *galapagensis*)	225-250	225(25)	3
Triaenodon obesus		120	4
Mobulidae			
Manta sp.		120	4
Muraenidae			
*_Gymnothorax berndti_	220-260	260(40)	3
*_G. nudivomer_	120-205	179(85)	2
*_G. nuttingi_	185-300	250(115)	3
Ophichthidae			
Myrichthys maculosus	150-215	185(65)	4
Synodontidae			
Unidentified synodontid		240	4
Holocentridae			
*_Myripristis chryseres_	135-240	155(105)	2
*_Neoniphon aurolineatus_		150	4
*_Pristilepis oligolepis_	165-345	230(180)	3
Ophidiidae			
Brotula sp. (*multibarbata* or *townsendi*)		230	4
Priacanthidae			
*_Cookeolus boops_	165-260	220(95)	1
Serranidae			
*_Anthias fuscinus_	135-280	215(145)	1
*_A. ventralis_		105	4
Callanthias sp.	240-330	285(90)	4
*_Epinephelus quernus_	135-350	230(215)	1
*_Grammatonotus laysanus_	310-350	335(40)	3
*_Holanthias elizabethae_	155-260	230(105)	1
*_H. fuscipinnis_	160-215	170(55)	1
Luzonichthys sp. (perhaps *earlei*)		105	4
*_Plectranthias helenae_	215-220	215(5)	3
Mugiloididae			
*_Parapercis roseoviridis_	215-270	245(55)	2
*_P. schauinslandi_	105-170	145(65)	1
Lutjanidae			
Aphareus furcatus	105-145	135(40)	2
*_A. rutilans_	190-250	220(60)	3
*_Etelis carbunculus_	245-365	310(120)	3
*_E. coruscans_	250-355	270(105)	3
*_Pristipomoides auricilla_	215-250	230(35)	3
*_P. filamentosus_	120-260	205(140)	3
*_P. zonatus_	205-295	240(90)	1
*_Symphysanodon maunaloae_	230-365	300(135)	1
Emmelichthyidae			
*_Erythrocles scintillans_	295-320	300(25)	4
Carangidae			
Carangoides orthogrammus	105-170	135(65)	2
Caranx lugubris	105-355	190(250)	1
C. melampygus	130-230	135(100)	2
Decapterus sp.		100	4
*_Elagatis bipinnulata_	90-150	120(60)	3
*_Seriola dumerili_	120-335	215(215)	1
Apogonidae			
*_Epigonus_ sp.	330-365	355(35)	2
Pomacentridae			
Chromis verater	120-140	130(20)	3
Mullidae			
Parupeneus cyclostomus		125	4
P. multifasciatus		125	4
Chaetodontidae			
*_Chaetodon modestus_	125-255	190(130)	2
*_C. tinkeri_	105-160	145(55)	3
Forcipiger flavissimus	125-145	130(20)	4
*_Heniochus diphreutes_	120-215	135(95)	2
Pomacanthidae			
Geniacanthus sp.		150	4
*_Holacanthus arcuatus_	130-150	135(20)	3
Labridae			
Bodianus bilunulatus	130-135	130(5)	3
Cheilinus unifasciatus		120	4
*_Polylepion russelli_	245-280	275(35)	3
Acanthuridae			
*_Acanthurus dussumieri_		130	4
*_Naso hexacanthus_	120-165	150(45)	2
*_Naso_ sp.	120-175	135(55)	1
Zanclidae			
Zanclus cornutus		125	4
Scorpaenidae			
*_Pontinus macrocephalus_	200-365	305(165)	2
*_Scorpaena colorata_		272	4
Scorpaena sp.	225-355	290(130)	2
Triglidae			
*_Satyrichthys engyceros_	355-365	365(10)	4
Bothidae			
Bothus mancus	270-350	310(80)	4
Balistidae			
*_Sufflamen fraenatus_	105-170	140(65)	1
Xanthichthys auromarginatus	115-155	135(40)	1
Monacanthidae			
Unidentified monacanthid		125	4
Tetraodontidae			
*_Canthigaster_ sp. (likely *inframacula*)	260-270	265(10)	4
Unidentified tetraodontid	135-150	145(15)	4
Ostraciidae			
Ostracion sp.		135	4
Diodontidae			
Diodon hystrix		135	4

nulatus, Acanthurus dussumieri, Zanclus cornutus, Xanthichthys auromarginatus, and *Diodon hystrix*. These fishes accounted for an increase in diversity at the 135 m dropoff. Similarly, due to the submersible's 365 m depth limit, lower bounds for some species are likely in error (e.g., *Symphysanodon maunaloae, Epigonus* sp., *Pontinus macrocephalus*, and *Satyrichthys engyceros*). Nonetheless, due to the large depth range sampled (100-365 m), the data still provide useful estimates of the depth distributions for most of the species listed.

The data suggest that large species have great



depth ranges. For example, all species with depth ranges exceeding 200 m are large (i.e., *Caranx lugubris*, *Epinephelus quernus*, and *Seriola dumerili*). Moreover, among extensively observed species, a significant Spearman correlation exists between ranked average weight and depth range (r_s = 0.52, df = 25, $P < 0.01$). This finding should be viewed with caution because of potential biases in depth distributions (see above).

The last column in Table 2 gives sighting scores for all species. Those assigned a value of 1 indicate species dominating the deep slope fish community in terms of species sightings. Note that some species were seen infrequently, but when encountered they were observed in large numbers (e.g., *Elagatis bipinnulata*, Fig. 4). Similarly, *Pristipomoides filamentosus* was not seen on every dive and was thus assigned an abundance score of 3. In spite of this, when seen, it was abundant and it was the most frequently caught while fishing (see next section). Sighting scores therefore do not indicate relative species' contributions to total standing crop biomass of the deep slope fish fauna.

Quadrat Sampling

A total of 974 quadrat sample counts were made during the 10 submersible dives. No attempt was made to estimate abundance separately for each species. Rather, the total number of bottom fish was recorded, regardless of species composition. Although severely reducing the detail of the data base, this did have the desirable effect of averaging biases due to attraction or repulsion of fishes to and from the *Makalii*. It was evident, for example, that some species were attracted to the submersible and followed it about (e.g., *Seriola dumerili* and *Caranx lugubris*), whereas others were repelled and actively avoided the submersible's lights (e.g., *Pristipomoides filamentosus* and *Etelis coruscans*). Still others did not seem to be greatly influenced (e.g., *Cookeolus boops*, *Epinephelus quernus*, *Pristipomoides zonatus*, and *Pontinus macrocephalus*). By pooling species quadrat counts, the abundance of some species was overestimated, some underestimated, and some estimated without bias. Due to averaging, we believe that pooled counts provide the best available estimates of total bottom fish density along the deep slope of Johnston Atoll.

FIGURE 4.—Johnston Atoll deep slope fishes. A. *Caranx lugubris* with wire coral; B. *Epinephelus quernus* peering out of cave; C. *Seriola dumerili* (foreground) and *Caranx lugubris* (background); D. school of *Elagatis bipinnulata* with *Carangoides orthogrammus* (above); E. *Heniochus diphreutes* with black coral; and F. aggregation of *Myripristis chryseres* and *Neoniphon aurolineatus*.

Some 367 bottom fish were counted in quadrat samples, resulting in a mean encounter rate of 0.38 fish/quadrat. The data were fitted to the Poisson distribution to ascertain the dispersion pattern. A chi-square goodness of fit test yielded χ^2 = 325.32, df = 3, $P << 0.005$, demonstrating nonrandom dispersion. The variance to mean ratio calculated from the frequency distribution of bottom fish/quadrat observations was 4.64 and was significantly greater than 1 ($P << 0.005$), indicating strong contagion.

One of the principal explanations for this result is shoaling by *Pristipomoides filamentosus* and *Etelis coruscans*. Both are large species, which formed aggregations of up to 100 individuals well off the bottom (20 m) in the vicinity of underwater headlands and promontories. These monospecific groups appeared to feed in open water on plankton, consistent with previous dietary studies of *P. filamentosus* (Kami 1973; Ralston[8]). When either was observed, there was an increased likelihood of encountering conspecifics. As a consequence 10 or more *P. filamentosus* were seen in one quadrat on 7 occasions.

Another factor contributing to clumping was nonrandom distribution with depth (Fig. 5). This figure presents the relationship between mean number of bottom fish per count and depth (vertical bars = standard errors). Note the two abundance peaks, the first at about 170 m and the second at 250 m. The former was due primarily to large numbers of *Caranx lugubris* and *P. filamentosus*. The location of the second peak was just below the second thermocline and was largely the result of local increases in numbers of *Epinephelus quernus* and *P. zonatus*.

The mean numbers of bottom fish per quadrat, stratified into 50-fathom depth intervals, are also shown in Figure 5 (i.e., 0.57, 0.47, and 0.06 fish/count). These data were converted to densities (1 quadrat = 0.003 ha) such that from 50 to 100 fathoms an average of 190 bottom fish are estimated to occur per hectare of habitat. Similarly, in the two deeper strata, estimated densities of 156 and 20 bottom fish/ha occur.

Given estimates of bottom fish density and depth-specific estimates of total available habitat (Table 1), estimates of the total standing crop of bottom fishes at Johnston Atoll indicate that about 339,000 fish occurred in the 50-100 fathom zone, 221,000 between

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[8] Ralston, S. Unpubl. data. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

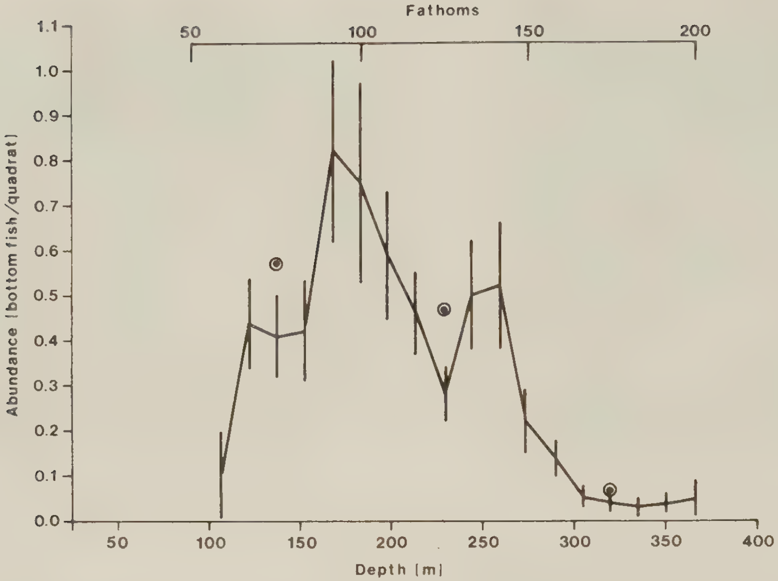

FIGURE 5.—The abundance of bottom fish (see text) in relation to depth. Solid line represents fish densities with changing depth (measured in meters or fathoms). Error bars are standard errors of means. Three 50-fathom depth zones are indicated, and mean fish densities within these are shown as circled points.

100 and 150 fathoms, and only 39,000 in the deepest (150-200 fathom) zone. Roughly 600,000 commercially exploitable bottom fish are estimated to comprise the deep-sea hook-and-line resource at Johnston Atoll. Because the fish are spread over a total habitat of 5,165 ha (Table 1), this corresponds to average densities of 118 bottom fish/ha.

Townsend Cromwell

Anywhere from 2 to 4 lines were deployed while fishing, resulting in an aggregate 41.8 line-h of fishing effort spread over 23 vessel drifts. A catch of 133 fishes (Table 3) produced an overall CPUE of 3.18 fish/line-h. Another 12 fish were hooked but lost to sharks before landing. All species caught while fishing were observed from the submersible with the exception of the bramid, *Eumegistus illustris*. Deepwater lutjanids predominated (69%), but substantial numbers of serranids (22%) and carangids (8%) were caught, a composition typical of tropical deep slope fisheries worldwide (Talbot 1960; Ralston and Polovina 1982; Munro 1983; Forster 1984).

TABLE 3.—Species composition of the bottom fish catch from the *Townsend Cromwell* at Johnston Atoll.

Family-species	Catch (*n*)	Percent	Average size (cm FL)
Lutjanidae (snappers)			
Pristipomoides filamentosus	43	32	54.4
P. zonatus	35	26	40.8
P. auricilla	5	4	34.6
Etelis carbunculus	5	4	51.2
E. coruscans	4	3	72.7
Subtotal	92	69	
Serranidae (groupers)			
Epinephelus quernus	29	22	69.8
Carangidae (jacks)			
Caranx lugubris	7	5	48.1
Carangoides orthogrammus	2	2	43.5
Seriola dumerili	2	2	79.5
Subtotal	11	9	
Bramidae (pomfrets)			
Eumegistus illustris	1	1	70.3
Grand total	133	101	

Species Composition By Location

Examination of catch data suggested a difference in species composition between upcurrent (sites 5 and 6) and downcurrent (sites 1-4) locations (Fig. 1). Landings were pooled into these two classes, and also by species category into *Pristipomoides filamentosus*, *P. zonatus*, *Epinephelus quernus*, and "others". The resulting 2 × 4 contingency table showed a lack of statistical independence between locations and species ($\chi^2 = 22.36$, df = 3, $P << 0.005$). Examining individual contingency table cells showed that the greatest contribution to the total chi-square was for *P. filamentosus* (58% of total). Specifically, under the hypothesis of independence, 16.5 were expected downcurrent but only 5 were caught, while 26.5 were expected upcurrent where 38 were landed. The apparent surplus of *P. filamentosus* along the eastern exposure, where trade winds prevail and oceanic currents first impact the atoll (Barkley 1972), may relate to this fish's habit of feeding on large deepwater plankton, especially salps (genus *Pyrosoma*). Bray (1981) has shown that small resident planktivores will travel to the upcurrent edge of a reef to access pelagic plankton. The distribution of *P. filamentosus* at Johnston Atoll may represent a similar situation on a much larger scale.

Bottom Fish Catch Rate

One-way analysis of variance (ANOVA) of CPUE data was used to examine whether geographical differences exist in bottom fish abundance, i.e., the two treatment classes were upcurrent and downcurrent regions (see above). The ANOVA was insignificant ($F = 1.62$, df = 1, 21, $P = 0.21$), although the mean catch rate along the eastern exposure (5.6 bottom fish/line-h) was 60% greater than downcurrent (3.5 bottom fish/line-h). This result suggests the lack of significance may have been due to small sample size.

The CPUE data were analyzed by time of day to determine if catchability fluctuates through the day. The results in Figure 6 show that fishing was distinctly better during the morning than afternoon. In this figure individual values of drift CPUE ($n = 23$) have been plotted against the midpoint of the drift time interval. The solid line represents aggregate catch rates, calculated by pooling both catch and effort statistics from all areas into 1-h intervals and then forming CPUE ratios. Different symbols represent each of six separate fishing locations (Fig. 1). Note that catch rates were highest when fishing began each day and consistently declined to a low during the midafternoon. The data further indicate that catch rates may increase again with the onset of the evening crepuscular period, although the data are meager. This pattern was evident both within and among the six sites fished and, when averaged out, resulted in morning catch rates 2.07 times greater than afternoon rates.

Catchability

Having the *Makalii* and *Townsend Cromwell* at Johnston Atoll at similar times prompts comparison of the assessment techniques. We assume that in the 1-mo interim between visits no changes occurred in overall levels of abundance, because Johnston Atoll is a National Wildlife Refuge where no fishing is permitted and the fishes are typically long lived (Ralston and Miyamoto 1983; Ralston see footnote 8). Any differences in assessment are then likely due to differences in method.

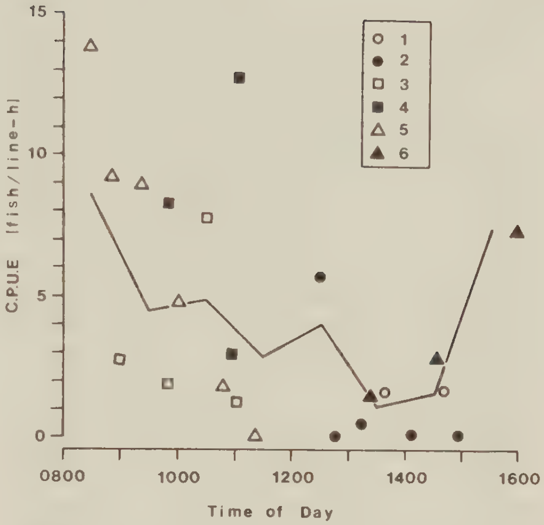

FIGURE 6.—The effect of time of day on the catch rate of bottom fish at Johnston Atoll. Catch rates calculated for each drift of the vessel and presented for each of six different fishing stations (see Figure 1).

To compare surface estimates of bottom fish abundance with those derived from submersible surveys, we matched fishing stations (numbers) with submersible dives (letters) which occurred nearby (Fig. 1). Specific pairings were F-1, E-2, B-3, H-4, I-5, and D-6. For each dive the overall abundance of bottom fish was estimated by forming the ratio of total fish counted to total number of quadrat counts, and then converting to density measured in bottom fish/ha. The CPUE statistics were used to estimate abundance for each fishing station, after correcting for fluctuating catchability (Fig. 6). The result is presented in Figure 7. There is a positive correlation between CPUE and bottom fish density ($r = 0.54$), although it is insignificant.

One means of estimating catchability, q, is to determine the slope of the regression of CPUE on stock density. We estimated the functional regression (Ricker 1973) of the data presented in Figure 7 (solid line) and determined that $q = 0.0215$ ha/line-h. A second estimate of q is obtained by forming the ratio of the average catch rate of bottom fish at the atoll

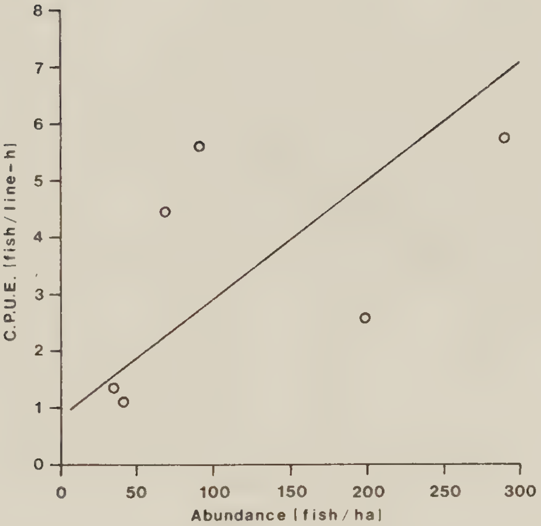

FIGURE 7.—The relationship between *Townsend Cromwell* CPUE and *Makalii* abundance estimates. Line fitted by functional regression. See text for further discussion.

(3.18 fish/line-h) to the average density of bottom fish viewed from the submersible (118 bottom fish/ha). The resulting estimate of q is 0.0269 ha/line-h.

DISCUSSION

The most enlightening aspect of this study was our ability to perform an in situ assessment of factors controlling the distribution and abundance of the deep slope biota at Johnston Atoll. Organisms showed not only distinct zonational patterns with depth but clumped dispersion along horizontal gradients as well.

The fish fauna of Johnston Atoll is often considered a depauperate outlier of the Hawaiian fauna (Gosline 1955; Randall et al. in press). In a later paper, Gosline (1965) examined vertical zonation in Hawaiian fishes, arguing that depth zonation patterns are often sharply demarcated in intertidal and shallow-water habitats, but these become increasingly attenuated with depth. The results of our study and Randall et al. (in press) support his conclusion (see also Forster 1984). Some deep slope species have extremely broad depth ranges (exceeding 200 m), yet few representatives of the shallow-water community extend appreciably beyond the 130 m escarpment encircling the atoll. Other investigators have noted that many Hawaiian species, which are commonly thought of as strictly associated with coral reefs, penetrate to depths well in excess of those favoring the growth of scleractinian corals (Brock and Chamberlain 1968; Strasburg et al. 1968; Clarke 1972). Yet the distributions of these fishes are limited largely to areas near the shelf break or shallower, while a true deep slope ichthyofauna, comprised largely of anthiids and lutjanids, exists along outer reef dropoffs at both Johnston Atoll and in the Hawaiian Islands.

Distributional patterns of fishes were nonrandom along horizontal gradients as well, as was readily apparent in the atoll-wide distribution of *Pristipomoides filamentosus* . Based simply on catch totals, 60% more *P. filamentosus* were expected to occur on the upcurrent exposure of the atoll than downcurrent, although 760% more were observed there, illustrating the clumped dispersion pattern which characterized this species during fishing surveys. Contagion was also evident in quadrat samples. Future studies would be well advised to incorporate statistical models consistent with these findings, including use of the negative binomial distribution to describe spatial patterns.

On a more local scale, it was clear from submersible observations that *P. filamentosus* and *Etelis coruscans* were concentrated near underwater headlands. Brock and Chamberlain (1968) made similar observations on deepwater populations of *Chaetodon miliaris*, attributing the very localized distribution of this species to increased accessibility of its food (plankton) in the vertical turbulence plumes formed by the impact of currents on underwater promontories. Because of its known planktivorous food habits, this hypothesis could explain abundance patterns of *P. filamentosus*. Moreover, fishermen emphasize the importance of currents in locating feeding aggregations of both *P. filamentosus* and *E. coruscans*. These two species taken together comprise the most important species landed in the Hawaiian deep-sea hook-and-line fishery, both in terms of yield and economic value. The relative abundance of these species in the deepwater bottom fish community may be due to their utilization of an allochthonous plankton resource transported to neritic waters from the open sea.

Bottom Fish Abundance

Certain methodological problems hindered this study and should be reviewed before comparing the abundance estimates from the two surveys. Any technique, including those used here, has its own specific combination of advantages and disadvantages.

There is ample reason to suspect bias in assessments based on underwater visual surveys. Sale and Douglas (1981) have shown that a single visual fish census seldom records all individuals present at the time of the census. Similarly, Colton and Alevizon (1981) showed that a quarter of the community they studied was characterized by significant diurnal changes in abundance. They concluded that unless sampling time is carefully controlled and standardized, results from visual abundance surveys may be seriously biased. Standardization was achieved in this study because all 10 dives started between 0840 and 0950 in the morning and each lasted 4 h. Furthermore, Brock (1982) showed that large, conspicuous, diurnally active species are accurately censused with visual assessment techniques, although the most abundant are often underestimated. With the exception of *Cookeclus boops*, which, although nocturnal, shelters in the open along the slope face, all of the species included in the quadrat sampling fit these criteria. Biases which frequently accompany visual assessments have thus been considered and minimized here.

Another factor which may have affected the results of *Makalii* surveys is attraction and repulsion of certain species to and from the submersible. Previous investigators have typically ignored this problem (Uzmann et al. 1977; High 1980; Powles and Barans 1980; Carlson and Straty 1981), while at the same time acknowledging that some species are attracted (e.g., black sea bass, southern porgy, Pacific halibut, sculpin, and yelloweye rockfish) or repelled (e.g., squid, herring, mackerel, butterfish, and wolf eel) to submersibles and divers. Nevertheless, as pointed out by Uzmann et al. (1977), one can at least observe the reactions of species to the submersible's presence, giving the viewer the opportunity to evaluate potential sources of error. We have attempted to address this problem by pooling counts for all species. While admittedly this procedure may not remove all bias, it is our feeling that in the absence of more quantitative information, little else can be done to improve the data. Studies are now being implemented to specifically evaluate the degree of attraction or repulsion of different species to the *Makalii*.

Provided an awareness of these concerns, the results presented here support the contention that the catch of bottom fish/line-h is a suitable CPUE statistic. This conclusion is based on the data presented in Figure 7, where CPUE generally increases with fish density and the regression intercept passes close to the origin. Although the relationship is statistically insignificant, this is likely due to small sample size ($n = 6$). Moreover, differences in bottom fish abundance between upcurrent and downcurrent locations were shown to result largely from the contagious dispersion of *Pristipomoides filamentosus* along the eastern side of the atoll, where its primary food resource first becomes available for consumption.

The estimation of catchability for deep-sea hook-and-line gear is a useful application of the dual sampling program presented here. The results suggest relatively great sensitivity of bottom fish stocks to exploitation pressure, a finding consistent with previous and ongoing studies (Ralston 1984). If we use $q = 0.0215$ ha/line-h as an estimate of catchability, we conclude that 1 line-h of *Townsend Cromwell* fishing effort removes about 2.2% of the bottom fish inhabiting 1 ha of habitat. A similar finding was reported by Polovina[9], who estimated q from the same vessel for a Mariana stock of bottom fish. Removals such as this are not insubstantial and underscore the importance of developing methods of stock assessment which can be used early in the development of a fishery and in the absence of conventional data sources. A combination of surface platform surveys with submersible ground-truthing is certainly a promising assessment technique to pursue (Uzmann et al. 1977).

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CHROMOSOMAL ANALYSIS OF ALBACORE, *THUNNUS ALALUNGA*, AND YELLOWFIN, *THUNNUS ALABACARES*, AND SKIPJACK, *KATSUWONUS PELAMIS*, TUNA

Chromosomal analysis is being used as part of an investigation of the population stock structure of the North Pacific albacore, *Thunnus alalunga*. There is a growing body of evidence (Brock 1943; Laurs and Lynn 1977; Laurs and Wetherall 1981; Laurs 1983) that North Pacific albacore are not as homogeneous as usually assumed (Clemens 1961; Otsu and Uchida 1963). Results from recent tagging studies suggest that northern and southern substocks constitute the North Pacific albacore population and that these proposed substocks have different migratory patterns (Laurs and Nishimoto 1979[1]; Laurs 1983). Laurs and Wetherall (1981) also found that the growth rates were significantly different in the two proposed substocks. In addition, the differences in growth rate are consistent with differences in length frequencies of albacore caught in commercial fisheries off North America (Brock 1943; Laurs and Lynn 1977).

In this paper we report results from chromosomal analysis using C-banding for albacore (from the proposed North Pacific southern substock) and compare them with similar results obtained for yellowfin, *Thunnus alabacares*, and skipjack, *Katsuwonus pelamis*, tuna. We demonstrate that there is a chromosomal basis for placing the albacore and the yellowfin tuna in the genus *Thunnus* and that recognizable chromosomal differences exist between the genera *Thunnus* and *Katsuwonus*. These findings corroborate the taxonomy of the albacore and the yellowfin and skipjack tuna based on comparative anatomy (Gibbs and Collette 1967; Collette 1978).

The results reported here are from part of a larger study, which is helping us to evaluate if genetic heterogeneity exists in the North Pacific albacore population. Information on chromosome characteristics is scarce for fishes, and to our knowledge this is the first time chromosome analyses have been reported for scombrid fishes.

Materials and Methods

All blood samples were collected from freshly caught fish either aboard the NOAA RV *David Starr Jordan* (August 1983) or aboard fishing boats

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[1] Laurs, R. M., and R. N. Nishimoto. 1979. Results from North Pacific albacore tagging studies. U.S. Dep. Commer., Natl. Mar. Fish. Serv., SWFC Admin. Rep. LJ-79-17, 9 p.

(October-November 1983). Because albacore have a high titer of red blood cells (Alexander et al. 1980), it was expedient to separate the lymphocytes from the erythrocytes. The lymphocytes were isolated from the blood on a density gradient of ficoll-sodium diatrizoate solution using a modification of the technique developed by Boyum (1968), which is specific for the concentration of lymphocytes. We found that it was necessary to isolate the lymphocytes and place them in culture within a couple of hours after blood samples were collected. The ficoll gradient procedure was not successful using undiluted heparinized blood that was retained for more than a few hours.

Two albacore, three skipjack tuna, and four yellowfin tuna were sampled. All fish were juveniles which have virtually no sexual dimorphic characteristics, and no sex determinations were made. The estimated fork lengths of the fish ranged from 65 to 85 cm for albacore, 80 to 120 cm for yellowfin, and 45 to 55 cm for skipjack.

From each fish, an 8-10 mL sample of blood was withdrawn via sterile intracardial puncture into a syringe coated with 1,000 units/mL of heparin. Two mL aliquots of blood were pipetted into each of the four 15 mL centrifuge tubes, and 4 mL of cell culture medium[2] was added. The mixture was centrifuged at 20 *g* for 5 min, and the white cells and plasma were transferred to another centrifuge tube. This procedure for the separation of the plasma and white cell mixture was repeated three times following the suggestions given by Blaxhall (1981).

Five mL of the white cell-plasma mixture were layered over 3 mL of ficoll-sodium diatrizoate solution and centrifuged at 572 *g* for 30 min. The overlaying plasma was removed carefully with Pasteur pipets, and the lymphocytes below were transferred to a culture tube containing 5 mL of marine teleost cell culture medium (Michael and Beasley 1973). This procedure resulted in an erythrocyte free culture of lymphocytes having a higher mitotic index. The cultures were incubated at 25°C for 3-5 d, at which time they were terminated and the cells harvested. The techniques for chromosomal analysis were patterned after those of Nowell (1960) for mammals because tuna are also endothermic (Graham and Dickson 1981). This work is an extension of the procedures developed by Kelly and Laurs (1983[3]).

Prior to harvesting the cells, 0.5 μg colcemid was added to 5 mL of culture medium and incubated for 2 h at 25°C. The culture was then centrifuged for 5 min at 180 *g* and the supernatant was replaced with 5 mL 0.075 M KCl for 10 min. The culture tubes were centrifuged again for 5 min at 180 *g*, and the supernatant was replaced with 3 mL of freshly prepared cold fixative which consists of 3 parts methyl alcohol to 1 part glacial acetic acid and mixed for 1 h. The tubes were again centrifuged at 180 *g* for 5 min, decanted, and fixed. The cell pellet plus 0.5 mL of fixative was retained for slide preparation.

Precleaned slides dipped in methanol and then in deionized water were used for slide preparations. Two drops of cell suspension were placed on the slide and 4 drops of fixative were immediately added. The slide was dried on a slide warmer at 37°C and stored at room temperature for 24-72 h prior to C-banding. The C-banding procedures were patterned after the work of Pardue and Gall (1970) and Arrighi and Hsu (1971).

In preparation for C-banding, the slides were placed in 0.2 N HCl for 15 min at 37°C, rinsed in deionized water, treated with saturated $Ba(OH)_2$ at room temperature for 7 min, and rinsed in deionized water. They were then immediately dipped again in 0.2 N HCl for 10 s and rinsed in deionized water. After the final rinsing the slides were incubated in 2× sodium chloride-sodium citrate solution at 60°C for 90 min and then stained for 90 min in Giemsa diluted with 1:10 Sorenson's buffer pH 6.8. Suitable metaphase figures were photographed at 1,008× magnification using a Zeiss[4] microscope equipped with a phase planapochromat 63/1.4 oil immersion lens.

Results

Chromosome Numbers

Kelly and Laurs (fn. 3) found that the diploid number of chromosomes for albacore was 48. We have confirmed this observation and have found that the diploid numbers for yellowfin and skipjack tuna are also 48. The modal frequencies of about 90 cells containing 48 chromosomes were 82.2% for albacore, 92.6% for yellowfin, and 80.5% for skipjack. Kelly and Laurs also observed that 85% of albacore cells had 48 chromosomes. Two polyploid cells with

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[2] RPMI-1640 Sigma Cat. No. R6504.

[3] Kelly, Raymond M., and R. Michael Laurs. 1983. Summary of methods developed for investigations of albacore chromosomes and of findings made on number of chromosomes. Unpubl. field and laboratory notes and results (April 1983). [Raymond M. Kelly, School of Medicine, University of California, La Jolla, CA; R. Michael Laurs, National Marine Fisheries Service, NOAA, La Jolla, CA.]

[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

96 chromosomes were observed in skipjack, and one polyploid cell with 96 chromosomes was observed in albacore. No polyploid cells were observed in yellowfin.

Chromosome Morphology

The albacore and the yellowfin and skipjack tuna were observed to have the same diploid chomosome number; however, their karyotype differed with respect to chromosome morphology. In this study, the chromosome pairs were arranged according to the morphology index (M), developed by Giannelli and Howlett (1967), which is obtained by dividing the length of the total haploid chromosome set p + q by the arm ratio (q/p). Based on our evaluation of 256 metaphase cells (Table 1), we found that the chromosome morphology of the yellowfin (Fig. 1) is more similar to that of the albacore (Fig. 2) than the skipjack (Fig. 3). The differences in chromosome morphology were most apparent in the three largest pairs of chromosomes (Table 1). The morphology index (M) places the metacentric and submetacentric chromosomes of the albacore and yellowfin in the number 1 and 2 positions respectively. Chromosome 3 of the albacore is also submetacentric while chromosome 3 of the yellowfin is referred to as subtelocentric. The subtelocentric category is used to describe chromosomes in which the centromeres are displaced more towards the telomere when compared with submetacentrics. The metacentric chromosome of the albacore was consistently larger than the metacentric of the yellowfin. The remaining 42 chromosomes were telocentric in the albacore and yellowfin. All of the chromosomes of the skipjack were telocentric.

C-Banding Patterns

C-banding determinations were done to differentiate individual chromosome characteristics among the three species of tunas (Table 2). The centromeric regions of most of the chromosomes of all three species contained C-band constitutive heterochromatin. However, there were differences in the intensities of staining on comparable chromosomes among the three species. Intercalary C-banding was observed only in the skipjack tuna and there was variability in terminal banding among the three species.

In the albacore all chromosomes, except pair 10, showed C-banding in the centromeric regions with intense, prominent bands notably apparent in chromosome pairs 2 and 3 (Fig. 2). Terminal banding was restricted to chromosome pair 1 which had obscure C-bands on one arm of each homologue. No intercalary C-banding was observed in the albacore. There were some minor differences in the C-banding patterns between albacore and yellowfin tuna. In the yellowfin, the centromeric regions of all chromosomes were banded, the intensity of the banding in the centromeric region was uniform

TABLE 1.—Classification of chromosome morphology for albacore and yellowfin and skipjack tuna.

Chromosome number	Albacore	Yellowfin	Skipjack
1	metacentric	metacentric	telocentric
2	submetacentric	submetacentric	telocentric
3	submetacentric	subtelocentric	telocentric
4-48	telocentric	telocentric	telocentric

TABLE 2.—Summary of C-banding characteristics for albacore and yellowfin and skipjack tuna.

Location of bands	Albacore	Yellowfin	Skipjack
Centromeric region	Present on all chromosomes except pair 10; intensely prominent on pairs 2 and 3	Present on all chromosomes with uniform prominent intensity	Present on all chromosomes except pairs 10 and 19, great variability in intensity most prominent on pairs 1, 3, 4, 7, and 18
Terminal bands	Present on one arm of each homologue on pair 1; weakly developed	Weakly developed on chromosome pairs 1, 3, 7, 8, 14, 15, 21, & 24	Notably prominent in pair 4
Intercalary	None present	None present	Present on all chromosome pairs except 17 and 24

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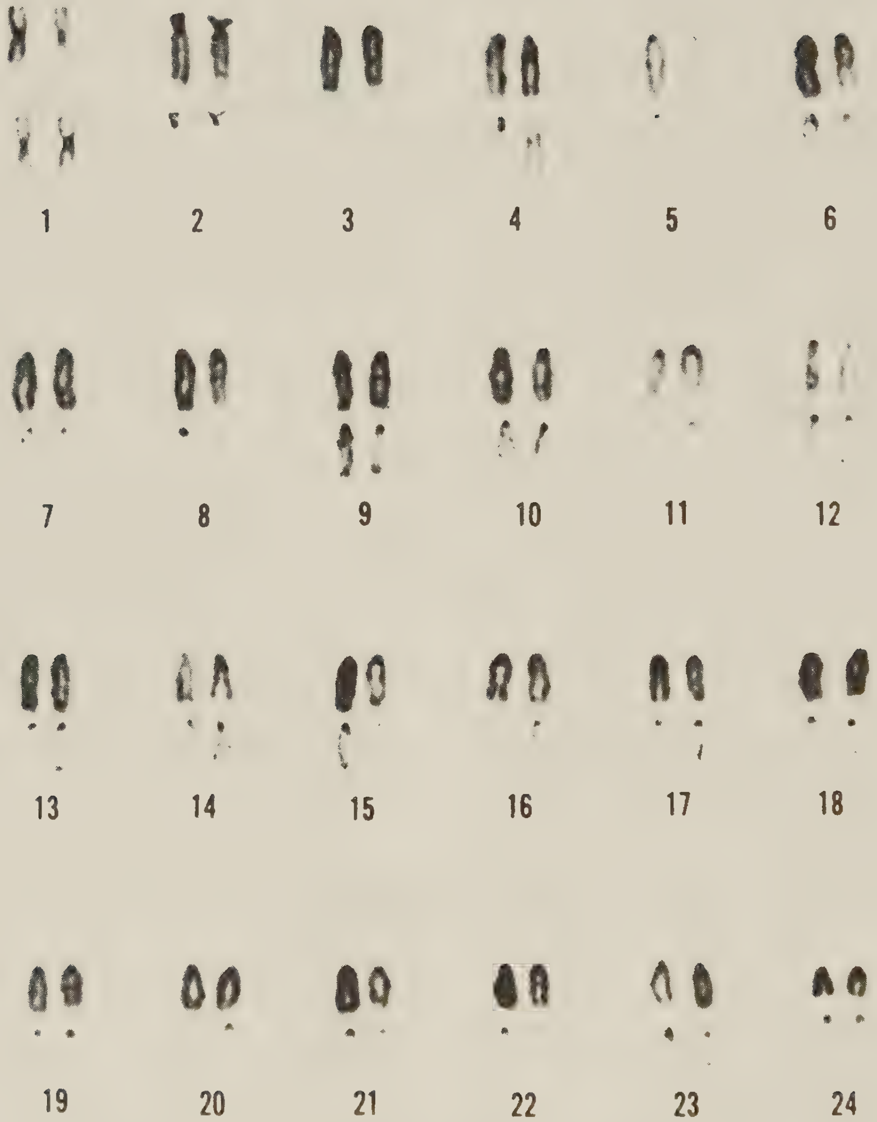

FIGURE 1.—Giemsa stained karyotype (upper row) and C-banding karyotype (lower row) of the same yellowfin tuna.

among all chromosomes, and terminal banding was weakly developed on eight pairs of chromosomes (Fig. 1). As in the albacore, no intercalary banding was observed in the yellowfin. The following significant differences were observed in the C-banding patterns between the skipjack and the other two species: 1) all chromosomes except 10 and 19 had C-banding in the centromeric region, 2) there was great variability in the intensity of staining in the centromeric region, 3) terminal banding was notably prominent in chromosome pair 4, and 4) there were intercalary bands on all chromosomes except pairs 17 and 24.

Discussion

Our results assist in understanding speciation processes that have occurred in the evolution of the

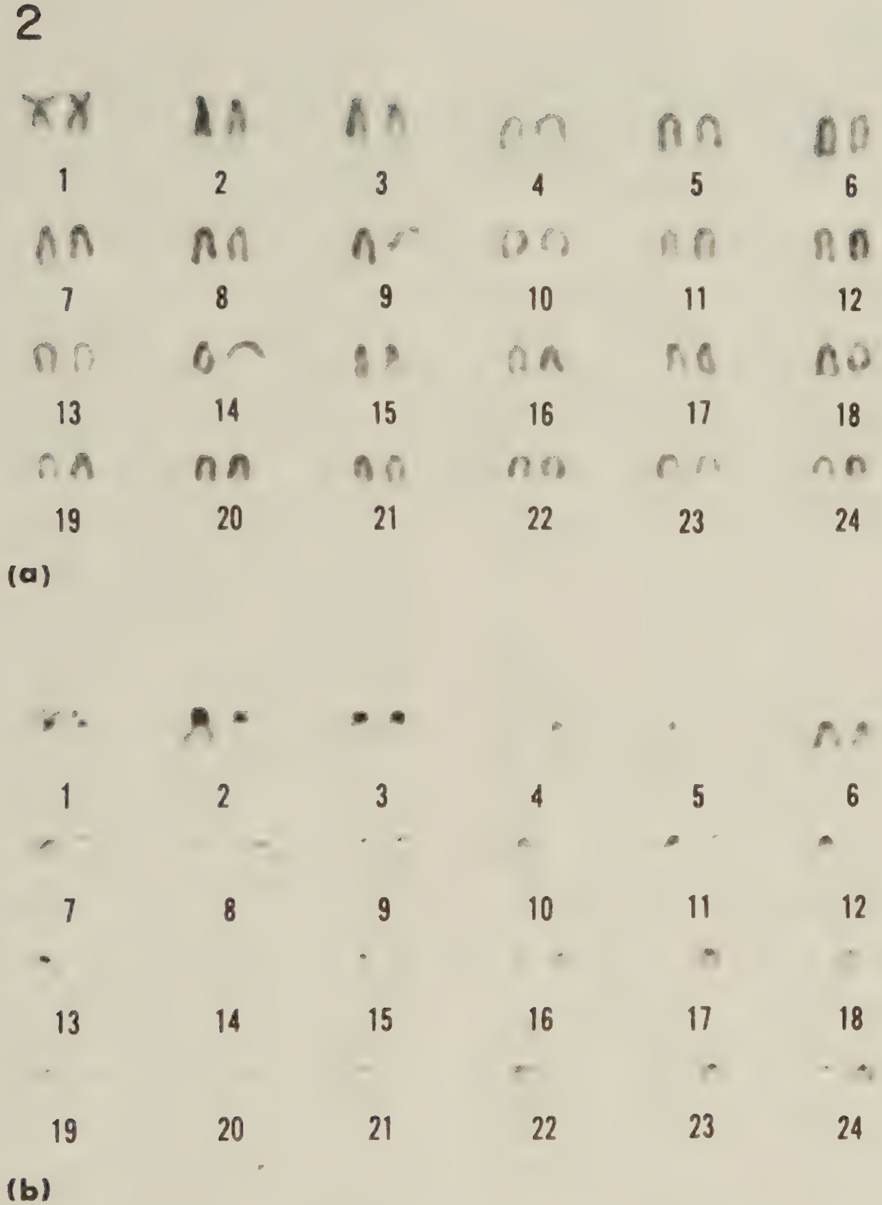

FIGURE 2.—Giemsa stained karyotype (a) and C-banding karyotype (b) from two different fish of the North Pacific albacore.

tuna. Gibbs and Collette (1967) proposed that seven species of tuna be included in the genus *Thunnus* on the basis of external morphological and internal anatomical characters. Our results demonstrate that there is a genetic basis for placing the albacore, *T. alalunga*, and the yellowfin tuna, *T. albacares*, in one genus *Thunnus* and the skipjack tuna, *Katsuwonus pelamis*, in a separate genus. These relationships are based on the assumption that closely related species will share certain karyotypic characteristics.

The determination that the albacore, yellowfin tuna, and skipjack tuna have the same number of chromosomes suggests that speciation of the genera of Thunnini might have occurred by intrachromosomal rearrangement as opposed to Robertsonian changes as hypothesized for the rainbow trout, *Salmo gairdneri* (Thorgaard 1976). If speciation had

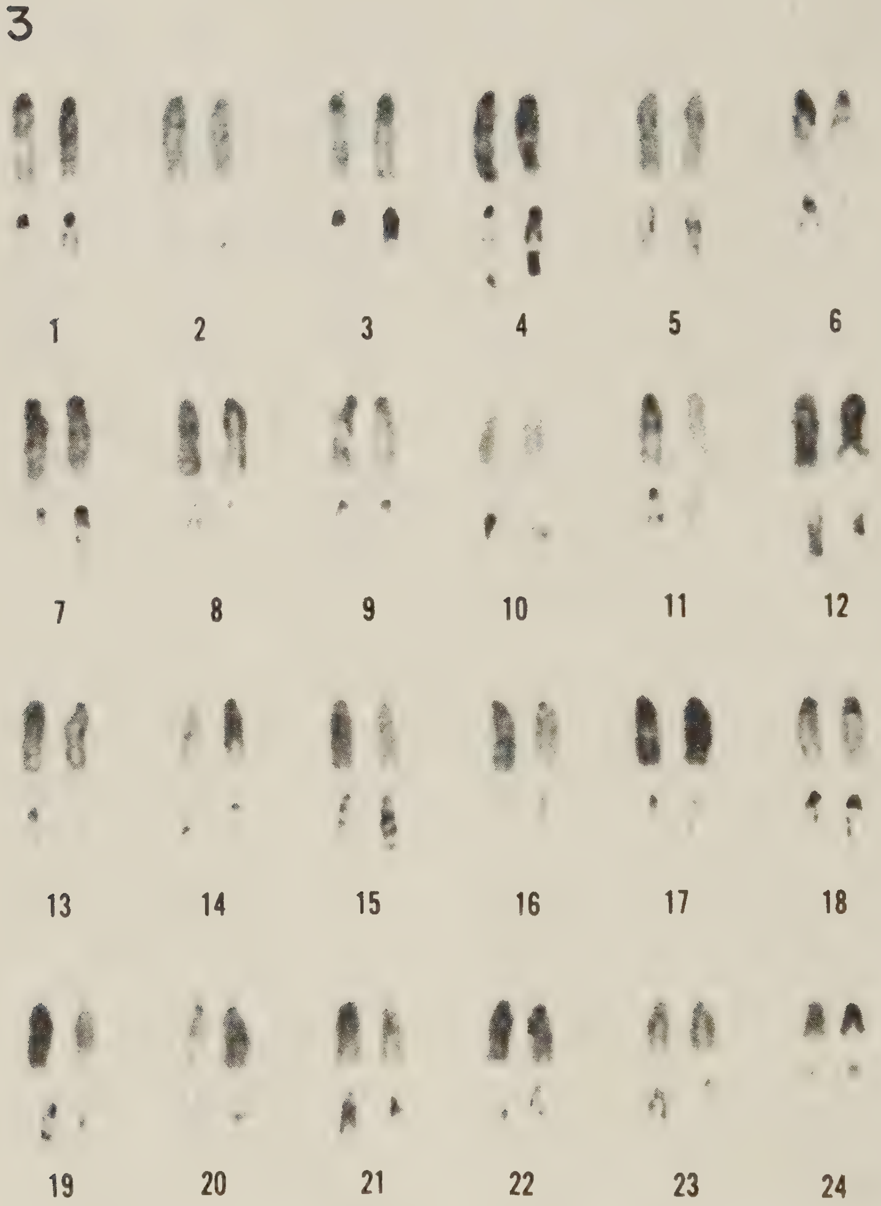

FIGURE 3.—Giemsa stained karyotype (upper row) and C-banding karyotype (lower row) of the same skipjack tuna.

involved a reduction in uniarmed chromosomes to form biarmed chromosomes, we would have expected to find a difference in the chromosome number between *Katsuwonus* and *Thunnus*.

It is probable that speciation within the genus *Thunnus* might also be related to chromosome rearrangement because the number of chromosomes is the same. Pericentric inversion is a type of intrachromosomal rearrangement that could result in the displacement of the centromere to convert a telocentric chromosome into a metacentric one. Zenzes and Voiculescu (1975) suggested that pericentric inversion was involved in the chromosomal organization of the brown trout, *Salmo trutta*. The extent to which this mechanism has been related to the speciation of genera *Thunnus* and *Katsuwonus* is uncertain. However, the occurrence of terminal C-bands on chromosome 1 of the albacore and chromosomes 1 and 3 of the yellowfin tuna is consistent with the hypothesis that these biarmed chromosomes were derived from a uniarmed condition. Indeed, White (1951) believed that, in grasshoppers, telocentric chromosomes are more primitive than the metacentric condition. Absence of terminal bands on chromosomes 2 and 3 of the albacore and chromosome 2 of the yellowfin tuna does not preclude the suggested derivation of metacentric chromosomes. It is possible that in the metacentric chromosomes lacking terminal bands, centrometric heterochromatin either was not moved or was lost. It is also possible that chromosome rearrangement in the speciation of the albacore and yellowfin occurred through changes in the euchromatic portions of chromosomes. To test this hypothesis it will be necessary to use G-banding techniques (Rishi 1978) to conduct analysis of these portions of the chromosomes.

In contrast to the albacore and yellowfin tuna, the telocentric chromosomes of the skipjack tuna showed a variety of intercalary and terminal C-banding in addition to those of the centromeric regions. An interesting condition was the polymorphic terminal heterochromatic block that occurred in chromosome pair number 4 of the skipjack, but not in the albacore or yellowfin. While the four specimens of skipjack analyzed had this polymorphism, it is not possible to comment on the frequency with which it might occur in the population. This type of differential banding also occurs in other fishes as demonstrated by Zenzes and Voiculescu (1975) who observed a difference in the size of C-bands in *Salmo trutta*. The C-band polymorphism we observed in skipjack could be related to the sex determining mechanism of the fish. However, we do not have any information on the sex of the skipjack used in this study and most fish do not have heteromorphic sex chromosomes (Zenzes and Voiculescu 1975; Thorgaard 1976; Kligerman and Bloom 1977). An exception occurs in the eels which have highly heteromorphic sex chromosomes (Park and Grimm 1981).

Analysis of C-banding patterns associated with the morphological differences in chromosomes has permitted us to identify all of the chromosome pairs of the albacore, yellowfin tuna, and skipjack tuna. We have demonstrated that karyotype analysis may provide a chromosomal basis for placing albacore and yellowfin in *Thunnus* and skipjack in *Katsuwonus*. Although C-banding techniques did not allow a detailed evaluation of the *Thunnus* chromosomes, we believe that the use of multiple banding procedures could provide important information on the speciation and cytotaxonomy of the species of this commercially important genus. In addition, use of G-banding procedures will be an important next step in determining if genetic heterogeneity exists in the North Pacific albacore population.

Acknowledgments

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F. J. RATTY

San Diego State University
San Diego, CA 92182

Y. C. SONG

San Diego State University
San Diego, CA 92182
Present address:
Wuhan University
Wuhan, Peoples Republic of China

R. M. LAURS

Southwest Fisheries Center
National Marine Fisheries Service, NOAA
P.O. Box 271,
La Jolla, CA 92038

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RATES OF INCREASE IN DOLPHIN POPULATION SIZE

Stephen B. Reilly and Jay Barlow[1]

ABSTRACT

Annual finite rates of increase in dolphin population size were estimated to vary up to a maximum of 1.09, using simulation, based on ranges in vital rates. Vital rate ranges were defined from values reported in the literature where possible, otherwise by making assumptions about biological or logical limits. Given information on current values, or limits, of one or more vital rate, one can use the figures presented to determine ranges of possible rates of increase in population size. The highest rates estimated here (up to 1.09) are probably unrealistic, because of the unlikely combinations of high fecundity and low mortality needed to achieve them.

Rates of increase in population size are important in determining management strategies for fish and wildlife subject to exploitation. A common management approach for setting incidental mortality or harvest quotas is to use a stock-production model (Schaeffer 1957; Allen 1976) with an assumed maximum rate of increase. For dolphins and other cetaceans, rates of increase have proven extremely difficult to measure directly. Nonetheless, estimates of this parameter are sometimes necessary, e.g., in setting incidental mortality quotas for dolphin populations involved in the eastern tropical Pacific purse seine fishery for yellowfin tuna (Smith 1983). In such situations, even a range, when rigorously defined, can contribute substantially to delineating the management options.

In this paper we define a range of reasonable values of rate of increase (hereafter also referred to as ROI) in dolphin population size, given what is known or can be inferred about their age-specific survival and fecundity distributions, or "vital rates". We estimate rates of increase using population projection matrices for various parameter combinations. We also suggest how the resulting ranges in ROI can be further narrowed, given specific information for an individual population.

There are many slightly different definitions for rate of increase, but all share the commonsense notion of change in population size over time. Caughley (1977) reiterated the distinction between exponential and finite rates: finite rates, here symbolized λ, are related to exponential rates, here symbolized r, by the simple conversion $\lambda = e^r$. (We use the term "finite rates of increase" for λ following Birch 1948.) Further, within exponential rates Caughley distinguished among "intrinsic" (r_m), "survival-fecundity" (r_s) and "observed" ($\bar{r}$), rates.

In this paper we compute a series of r_s values, resulting from ranges of survival-fecundity distributions. The highest value of r_s resulting from the range of vital rates considered is our best estimate of dolphin r_m, or "r-max".

We define the ranges in vital rates based on the literature for dolphins where possible. Otherwise, we rely on information for other large mammals and what appear to be logical or biological limits.

There are two previous studies of a similar nature for delphinids. As part of a general review of life history analysis of large mammals, Goodman (1981) examined the relationships among rate of increase, juvenile and adult survival rates. He looked at single values for calving interval and age at first reproduction across ranges of survival rates. We take a broader look at these relationships, examining ranges for all four parameters.

Polacheck (1984) examined interparameter relationships for eastern tropical Pacific (ETP) dolphins, *Stenella* spp., given specific vital rate estimates available as of 1981, showing the values were not consistent with a positive population growth rate. Since then, revised estimates have become available for some relevant parameters, and this specific case has been reanalyzed, with similar general conclusions.

The only reported dolphin rates of increase are for *Stenella coeruleoalba*. For the year 1974, Kasuya (1976) estimated a rate of 0.024 for the population off Japan. This value was computed in a complex manner, based on an observed fishing mortality, assumed natural mortality, and estimated popula-

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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tion size, calving interval and sex ratio. Assuming that calving interval was density dependent, Kasuya (1976) estimated a maximum annual rate of increase of 0.044 for this population of *S. coeruleoalba*.

METHODS

The Model

Population growth rates are estimated here using the familiar Leslie matrix model (Leslie 1945). A simplified parameterization is used for which survival rates and fecundities remain constant over many age classes. Four parameters are required: 1) calving interval for reproductively mature females, 2) average age at first birth for females, 3) annual adult (noncalf) survival rate, and 4) annual calf survival rate. This degree of detail corresponds to the practical limitations in collecting data on wild dolphin stocks.

The model is constructed with the assumption that age class 1 corresponds to newly born calves (i.e., censuses occur immediately after the calving season). In fact, the model is not dependent on discrete calving seasons, but this assumption helps in conceptualizing some elements of the model. The fecundities (elements of the first row of the Leslie matrix) represent the number of female calves born in one year per female of a given age class in the previous year. Fecundities for mature age classes are estimated as the annual pregnancy rate (the inverse of calving interval) multiplied by the adult survival rate (the probability that a [pregnant] female will survive to the calving season) multiplied by 0.5 (the fraction of female offspring). The annual pregnancy rate is estimated as the percent of sexually mature females which are pregnant, divided by the gestation period (in years).

The choice of only two different survival rates for all life stages was made because of data limitations for dolphins. Perhaps a more biologically reasonable assumption would be that dolphins have a U-shaped mortality curve which is characteristic of mammals in general (Spinage 1972; Caughley 1977; Siler 1979; Smith and Polacheck 1981). Barlow[2] incorporated this typical mammalian survivorship curve in models of growth for spotted dolphins, *Stenella attenuata*. Our choice of a separate survival rate for calves was based on the common observation of higher mortality in juvenile mammals (Caughley 1977; Siler 1979). For convenience, juvenile mortality factors are compressed into the first year's survival rates. This simplification is justified because population growth rates do not depend on the age at which juvenile mortality actually occurs. We recognize that juvenile mortality factors probably extend past the first year of life, but insufficient data exist to justify including this in our model. Higher mortality in old age was not incorporated in our model, but maximum age was limited to 50 yr. The survival rate at age 50 was thus zero.

We calculate population growth rates for a range of the four vital rate parameters mentioned above. Finite population growth rates, λ, that are associated with these parameter values were calculated by solving Lotka's characteristic equation, using Newton's method. The explicit form of Lotka's equation used is

$$1 = \sum_{x=1}^{50} \lambda^{-x} l_x m_x$$

where l_x is the survivorship from birth to age class x and m_x is the fecundity of age class x.

Below, we define the ranges used for the four population parameters and describe how they were selected.

Survival Rates

Ranges in Noncalf Survival Rates

Few estimates of adult survival rates for dolphins are available in the literature, primarily because adequate data are difficult to collect. Kasuya (1976) presented annual survival rate estimates of 0.925 and 0.882 for exploited populations of *Stenella attenuata* and *S. coeruleoalba*, respectively; however, his method (log-linear regression) is biased (Barlow 1982), and he did not adjust for the effect of population growth on age structure. A range of 0.85 to 0.97 was chosen for survival rates in this study. Values <0.85 do not allow population growth for the ranges of other parameters appropriate here, hence these values were not considered. Values higher than 0.97 result in more than 22% of the population being over 50 yr old. This is inconsistent with estimates of longevity for delphinids based on tooth layer counts [58 yr in *S. coeruleoalba* (Sacher 1980), 38 yr in *S. attenuata* (Hohn and Myrick[3])], hence values

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[2] Barlow, Jay. 1986. Biological limits on current growth rate of a spotted dolphin population (*Stenella attenuata*). Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

[3] Hohn, A. A., and A. C. Myrick, Jr. 1986. Age distribution of the kill of spotted dolphins in the eastern tropical Pacific.

>0.97 are untenable as mean per-capita survival rates.

Ranges in Calf Survival Rate

Again little information is available on calf survival for dolphins. Kasuya (1976) estimated a juvenile survival rate that was higher than that of adults, based on a balance equation. His methods assume that populations are neither growing nor declining, and he did not show that this assumption was met. Also his juvenile period included all sexually immature age classes. The overwhelming body of evidence from terrestrial mammals is that very early juvenile mortality is higher than adult mortality (Spinage 1972; Caughley 1977; Siler 1979). Even human populations had a first year survival rate of <0.88 prior to modern antibiotics (Fruehling 1982, data for U.S. circa 1900). An upper limit on calf survival rates was generated by assuming a calf is absolutely dependent on its mother for 1 yr. A calf has the same risk of dying as an adult, plus the additional risk of dying of starvation if its mother dies before completing 1 yr of lactation. The upper limit on calf survival would thus equal the square of the adult survival rate. The lower limit on calf survival rates was chosen as 0.50, a value that seems typical of pinnipeds (Smith and Polacheck 1981) and long-lived terrestrial mammals (Spinage 1972).

Fecundity-Related Rates

Ranges in Calving Interval

Observed calving intervals for dolphins generally range from 2 to 4 yr (Perrin and Reilly 1984); consequently, we have used this range in our computations. Intervals reported for killer whales (which are also delphinids, but not "dolphins") are considerably longer, up to 8 yr (e.g., Jonsgård and Lyshoel 1970).

The literature includes reports of calving intervals <2 yr for dolphins. These reports do not appear to be valid. Reevaluation of data for three of these reports[4] indicates that sampling was biased toward pregnant females (Perrin and Reilly 1984), a result of what may be a general tendency for dolphins to segregate by age/sex groupings[5].

The remaining reports of calving intervals <2 yr are from very small sample sizes.[6] Gestation periods for dolphins are at minimum 10 mo, and intraspecific variation is small. Reported lactation periods range from 1 yr to over 2 yr (Perrin and Reilly 1984). Summing these two periods gives another indication that dolphin calving intervals are not likely to be <2 yr.

An exception to the 2-yr minimum calving interval would possibly be in a population experiencing very high calf mortality, causing premature cessation of lactation, and allowing females the opportunity to begin a new calving cycle (assuming there was no seasonality to breeding which could require a resting period before the next breeding season). To include consideration of this case we would need to devise an arbitrary function relating low calf survival to short calving intervals. The net result would again be low rates of increase. To avoid such complications we have simply used 2 yr as the minimum average calving interval.

Ranges in Age at First Birth

The available data suggest a range in age at attainment of sexual maturity of 6 to 12 yr for dolphins (Perrin and Reilly 1984). Early reports of Black Sea common dolphins, *Delphinus delphis*, attaining sexual maturity at an average of 3 yr (Kleinenberg 1956) are almost certainly due to faulty age determination[7]. Because of the recent findings for *S. attenuata* from the ETP (Myrick et al. 1986), we considered the ages at first birth up to 15 yr. In our formulation of the Leslie model, if females mature and first conceive at an average age of 10 yr, the first nonzero fecundity would be in age class 11 (Table 1).

TABLE 1.—Parameters used and values included in the computation of rates of increase in dolphin population size.

Parameter	Values
Calving interval	2 yr 3 yr 4 yr
Age at first birth	7 yr 9 yr 11 yr 13 yr 15 yr
Calf survival rate	0.50 0.52 0.54 . . . $(Sa)^2$
Noncalf survival rate (Sa)	0.850 0.855 0.860 0.865 . . . 0.970

Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

[4] Three reported cases of dolphin calving intervals <2 yr, later found to be biased due to age and sex segregation, are Black Sea *Delphinus delphis* and *Tursiops truncatus* (Kleinenberg 1956) and Western Pacific *Stenella coeruleoalba* (Miyazaki and Nishiwaki 1978).

[5] Hohn, A. A., and M. D. Scott. 1983. Segregation by age in schools of spotted dolphins in the eastern tropical Pacific. Fifth Biennial Conf. Biol. Mar. Mammals, Abstr., p. 47.

[6] Henderson, J. R., W. F. Perrin, and R. B. Miller. 1980. Rate of gross annual reproduction in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973-78. Southwest Fisheries Center, La Jolla, California, Admin. Rep. LJ-80-02, 51 p.

[7] Myrick, A. C. Jr., Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038, pers. commun. June 1984.

RESULTS

Figures 1 through 5 give finite rates of increase (displayed as $(\lambda - 1) \cdot 100$) for the above ranges of age at first birth, calving interval, and calf and noncalf survival. The lower left corner of each panel is blank because we did not consider cases where calf survival exceeded the square of noncalf survival, for the reason discussed in Methods.

The maximum finite rates of increase which would result from the parameter ranges included here are 1.08 to 1.09. Rates as low as 0.89, i.e., decrease of 11%/yr. also resulted from the parameter ranges used.

Within the ranges of parameters examined here, rate of increase is most sensitive to calving interval and noncalf survival rate, followed by age at first birth, and is relatively insensitive to changes in calf survival rate. This is an expected result following the reports by Eberhardt and Siniff (1977) and Goodman (1981). An increase in calving interval of 1 yr results in a decrease in ROI of about 0.02, holding other parameters constant. For example, the maximum ROI for a 9 yr age at first birth is about 1.07 with a 2 yr calving interval. This ROI drops to 1.05 with a 3 yr calving interval. A decrease of 0.01 in noncalf survival rate results in a 0.01 decrease in ROI, while a 0.10 decrease in calf survival rate decreases ROI by <0.01. Age at first birth appears to be nonlinearly related to ROI over the ranges examined here. An increase in this age from 7 to 9 yr results in a 0.02 decrease in ROI, while an increase

FIGURES 1-5.—Contours of percent rate of increase in dolphin population size ($(\lambda - 1) \cdot 100$), as a function

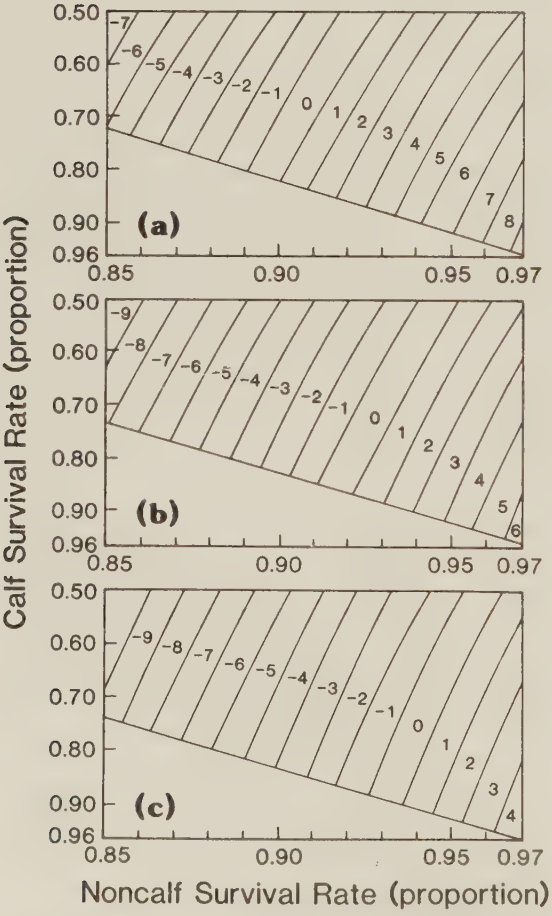

FIGURE 1.—First reproduction of dolphin age class 7 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

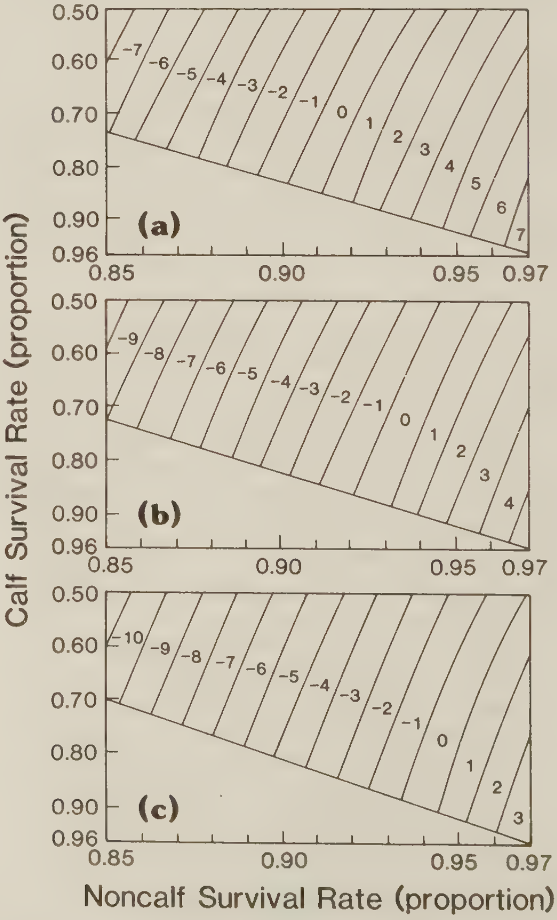

FIGURE 2.—First reproduction of dolphin age class 9 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

from 11 to 13 yr causes only a 0.01 decrease in ROI.

DISCUSSION

The ranges of rate of increase estimated here are potentially useful in bracketing possible ROIs for delphinids in general. For any particular population it should be possible to further narrow the range of likely values of ROI, given available estimates for vital rates. For example, *Tursiops truncatus* from the northeast coast of Florida reportedly attain sexual maturity at 12 yr on the average (Sergeant et al. 1973) and have a 12-mo gestation period (Essapian 1963), giving an estimated age at first birth of 13 yr. Knowledge of this single parameter can narrow consideration to Figure 4. Here the estimated range in ROI is up to a maximum of 1.05, for the extreme case of an average calving interval of 2 yr, and noncalf survival >0.96. Additional knowledge of, say, minimal calving interval for *Tursiops* could further narrow consideration to one of the three panels of Figure 4, and establish minimal survival rates for positive growth rates, or the maximum rate of increase possible, given the above constraints on age at first birth and calving interval.

We assume that the ranges defined here also encompass the limits within which vital rates for any one dolphin species might change in response to changes in population density. This obviously entails making simplistic assumptions about density dependence in vital rates, and therefore in rate of increase.

of calf and noncalf survival rates, for the following combinations of calving interval and age at first reproduction:

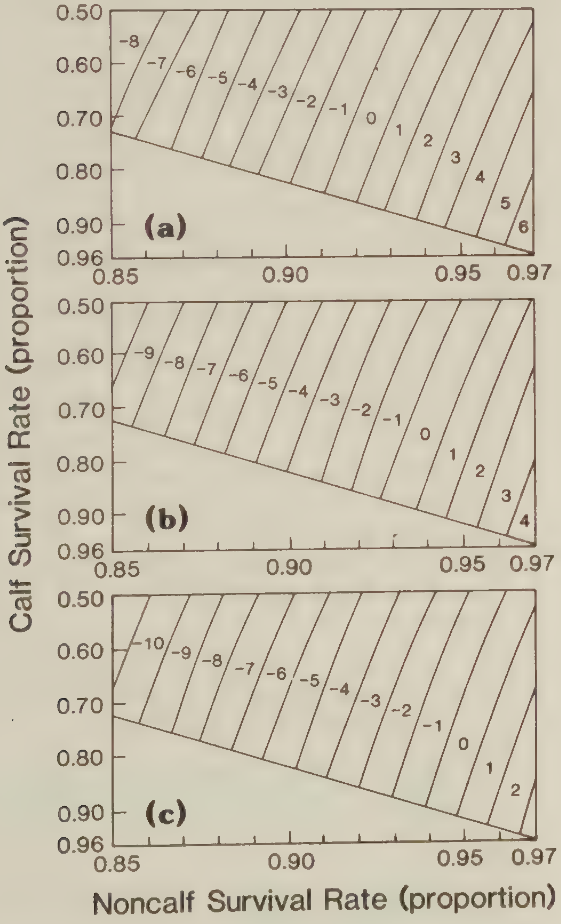

FIGURE 3.—First reproduction of dolphin age class 11 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

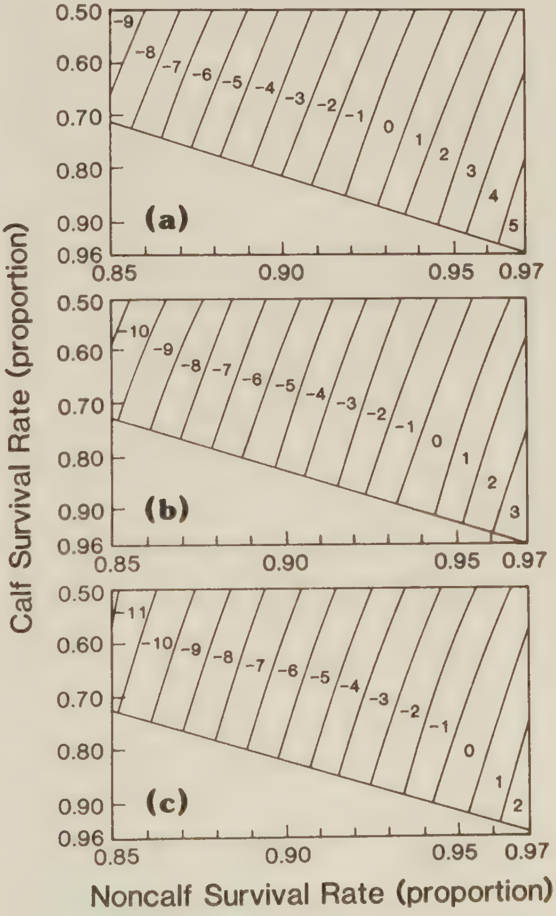

FIGURE 4.—First reproduction of dolphin age class 13 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

These assumptions are implicit in the concept of r-max.

There is no evidence that the highest rates of increase calculated here can be achieved by any real dolphin population. Trade offs may exist between survival and reproduction. Because of this, some of the parameter combinations examined here are probably unlikely, especially combinations of the extreme values, i.e., those producing the highest rates of increase.

Although our figures also present minimum values based on parameter combinations we used, we do not believe that these will be useful in setting lower bounds on finite rates of increase. Catastrophic events can always lead to rapid extirpation of a population. In fact, it is clear that dolphins (and other animals with similar life histories) can decrease in number much faster than they can increase.

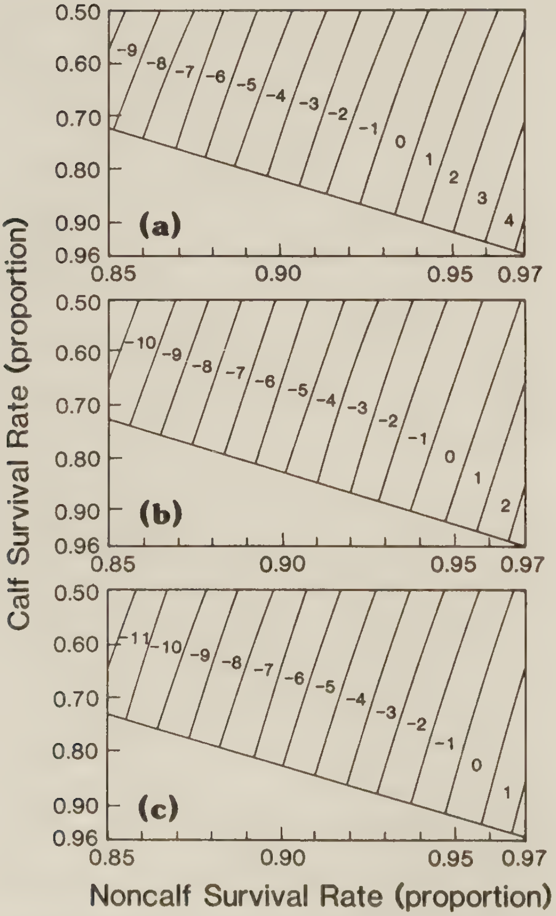

FIGURE 5.—First reproduction of dolphin age class 15 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

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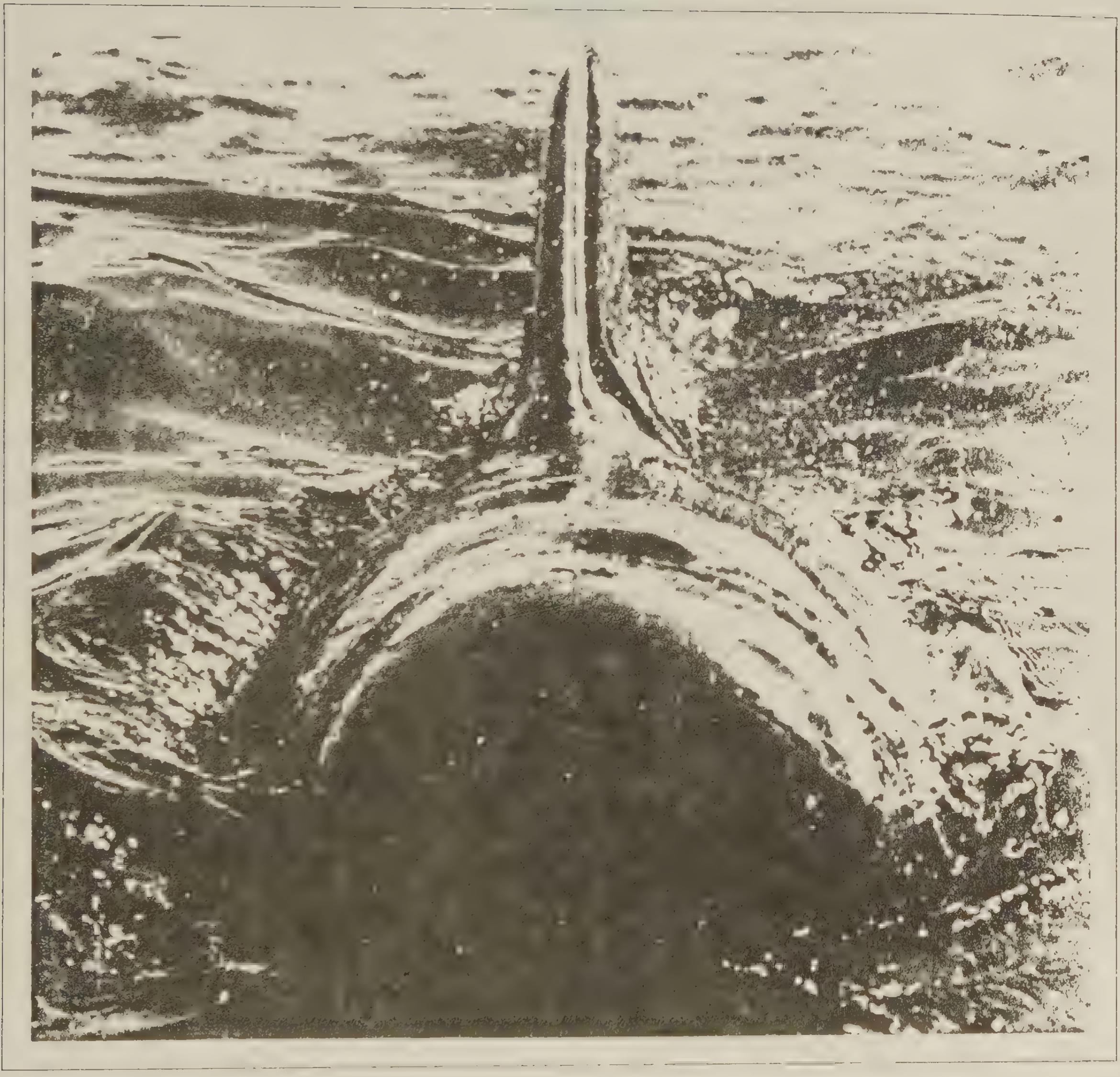


A pilot whale meets the camera head on. The frontal bulge, or melon, on its head is thought to contribute to this whale's acoustic abilities.
(Susan H. Shane)

Pilot Whale

by Stephen B. Reilly and Susan H. Shane

The pilot whale *(Globicephala macrorhynchus)*—with a variety of common names, an unsettled taxonomic status, and many gaps of information in its life history—is a creature of confused identity. (The confusion is ours, of course.) Some of its characteristics, however, are undisputed: it is among the most sociable and intelligent of the cetaceans. In captivity, it has proved itself at least as intelligent as the well-known bottlenose dolphin. In the wild, the gregarious pilot whale is usually found in groups whose social structure seems to be highly organized.

Pilot whales are known by many names, including "potheads," a term which refers to their bulbous, blunt heads, and "blackfish," which reflects their dark appearance. In the eastern Atlantic, they associate with schools of herring, and, because fishermen there came to believe that the whales were "calling" them to fish, the whales became known as "caa'ing" whales. The name "pilot whale" is said to have a similar origin—a popular belief that the whales would "pilot" fishermen to their catch. Another theory relates to the presumption that pilot whales often have a leader or "pilot" at the head of their pods.

Pilot whales are, in effect, large dophins. Most scientists place them in the same family with the dolphins and porpoises (Delphinidae). Taxonomists do not agree about correct classifications of groups or about distinctions among the various pilot whale forms. Nevertheless, wherever they are found, pilot whales are similar. As a result of this basic similarity, some types of information obtained about pilot whales in one area may serve as a good indication for all.

Pilot whales are predominantly black with their most distinguishing features being a blunt, bulbous head and a widely based, squat dorsal fin, which is set far forward on the body. Calves are gray in color. Some forms of this genus (including those off the Pacific coast of North America) have a gray or white saddle-shaped area just behind the dorsal fin. On the chest, potheads have a gray or white anchor-shaped patch, which is sometimes connected by a narrow blaze to a grayish white area around the genitals. Also distinctive of this cetacean are its long, sickle-shaped pectoral fins. It has been suggested that a famous 1934 photograph of Scotland's Loch Ness monster is remarkably similar to the sight of a pothead lying on its side at the water's surface and waving a pectoral fin in the air. The very long tail stock is laterally compressed, thus forcing beached animals to lie on their sides rather than on their bellies. When the whale begins a long dive, the tail stock is exposed in an arching roll, which is frequently followed by the appearance of its small dark tail flukes.

Although subadult males and adult females are indistinguishable in the field, the adult male is significantly larger in all proportions than the adult female. The male has a larger melon, which protrudes beyond the upper jaw, a more deeply keeled tail stock, and a thicker leading edge on the dorsal fin. In the North Pacific, males generally reach a length of about twenty feet and females reach only fifteen or sixteen feet.

Pilot whales are sometimes confused with other whales, such as the false killer whale, which reaches comparable lengths, is black, and is sometimes called "blackfish." However, the body of the false killer is considerably less robust. Its head is smaller and gently tapering, and its dorsal fin is taller, more narrowly based, and set farther back on the body. False killer whales also sometimes ride the bow waves of boats—a skill that pilot whales are not known to practice. Off southern California, inexperienced observers often mistake Risso's dolphins *(Grampus griseus)* for pilot whales. These dolphins, however, have tall pointed dorsal fins and distinctly whitish heads.

Generally pilot whales are found in the world's tropical and temperate oceans. They are more abundant where schooling squid—their preferred food—are found. In turn, pilot whales are the prey of sharks, humans, and perhaps killer whales. Along the Pacific coast of North America, pilot whales are most abundant south of Point Conception (just northwest of Santa Barbara, California). From there north to the Gulf of Alaska, they are only rarely sighted; these infrequent movements north of Point Conception may be related to seasonal influxes of warmer temperate waters.

In southern California, there is a traditional aggregation of a few hundred pilot whales each winter at Santa Catalina Island. The whales come to feed on spawning market squid. In the winter of 1983–84, when the warm waters of the most severe El Niño on record affected the marine ecosystem, the squid failed to gather at this island for spawning, and the potheads failed to make their annual appearance for the first time on record. Although water temperatures were restored to normal the following winter, the residual effects of El Niño resulted in only a small number of spawning squid at Santa Catalina Island, and only one pod of twenty potheads spent the winter there. The location of most of the pilot whales during these two winters remains a mystery, although it is likely that they moved farther offshore.

In the Atlantic, there are two well-defined species of pilot whales, distinguished by differences in distribution, skeletal and external morphology, and coloration. *Globicephala melaena* is called the long-finned pilot whale because its pectoral flippers reach at least one fifth of the length of its adult body. The other Atlantic species, *G. macrorhynchus*, is called the short-finned pilot whale because the pectoral fins of adult animals are up to one sixth of the total body length. Some overlap does occur in these characteristics. The distributional boundaries between the two Atlantic species are relatively well defined. The long-finned pilot whale's distribution is "antitropical"—located in temperate waters to the north and south of the generally tropical short-finned pilot whale.

Unfortunately, our knowledge of pilot whales in the Pacific is less complete. There are at least two, possibly three, distinct forms present. The long-finned variety, *G. melaena*, ranges north from the Antarctic convergence along the west coast of South America to Peru, in the cold Humboldt Current. Subfossil material discovered in Japan indicates

A breaching pilot whale shows its sickle-shaped flippers. (Susan H. Shane)

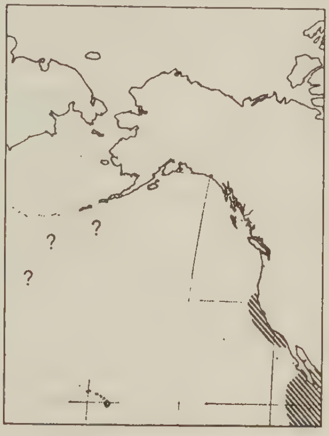
that *G. malaena* was present in the North Pacific as recently as the tenth century.

Some controversy currently surrounds the eastern North Pacific form. The short-finned pilot whale, *G. macrorhynchus*, is variously described as being tropical (as this species is also in the Atlantic and Indian oceans) and as occurring from about Guatemala north to the Gulf of Alaska. Most investigators consider the eastern North Pacific form to be the same as the pilot whale of the tropical Pacific, *G. macrorhynchus*, while a few have labeled it a separate species entirely, most often *G. scammonii*. The basis of this problem is as old as the study of biology: Just exactly what defines a species? Unfortunately, not all biologists accept the same set of criteria. The identity of the North Pacific pilot whales is a case in point.

In 1971 Dutch cetologist P. J. H. van Bree compared skull measurements of a number of proposed species of pilot whales and, finding no significant differences, concluded that all tropical and temperate North Pacific pilot whales are of the same species: *G. macrorhynchus*. In 1981 a statistical analysis of all available Pacific pilot whale skulls by James Polisini of the University of Southern California, essentially confirmed Van Bree's finding. While acknowledging the similarity of skull characteristics, other scientists point out the larger overall size of the North Pacific form, its temperate distribution, larger melon, and flipper length intermediate between that defined for the short-finned and long-finned species. Because of these apparent differences, a few biologists continue to recognize *G. scammonii*. The problem is compounded by the fact that both of these types—*G. macrorhynchus* and *G. scammonii*—seem to occur together along Baja California and off southern California, and near Japan, as well.

Squid is the pilot whale's major food, although when squid are not available, some fish are consumed. A current theory holds that, in the toothed whales that consume primarily squid, there is an evolutionary trend toward reduction in the number of teeth. While the predominantly fish-eating spotted dolphin has a total of 150 to 160 teeth, and the white-sided dolphin has 100 to 110, the squid-eating pilot whale has 28 to 48. Other squid eaters, such as the Risso's dolphin and the beaked whales, have 4 to 12 and 0 to 4 respectively. This theory argues further that teeth are not necessary to capture densely schooling squid; teeth may even interfere with the process of engulfing large numbers of the prey.

Like other cetaceans, pilot whales generally swallow their food whole, without chewing it, and probably ingest using strong suction. A typical eighteen-hundred-pound adult female pilot whale fills her three-chambered stomach with twenty-five to thirty pounds of squid. If, as has been estimated, she requires eight hours for complete digestion, she may fill her stomach two to three times each day. Thus, an average mature female pothead may consume fifty to ninety pounds of food daily.



Pilot whale distribution

▨ Major concentrations

While we currently know almost nothing of the life history of eastern North Pacific pilot whales, those of the western North Pacific (off Japan) have been studied in detail by Toshio Kasuya of the Far Seas Fisheries Research Laboratory in Shimizu and Helene Marsh of James Cook University in Australia. These researchers have found that breeding is diffusely seasonal, with a single peak of conceptions in April and May, and a single peak of births in July and August. Gestation lasts about fifteen months. Breeding seasonality is probably related to the females' reproductive cycle, since they showed a peak in ovulations coincident with the spring peak in conceptions, while there was no clear evidence of seasonality in the sexual condition of males.

As with other marine mammals, one calf is born at a time. Most young pilot whales studied in the western North Pacific are suckled for at least two years, while calves of older cows may be nursed for considerably longer. Females mature at nine years on average and usually have four or five calves, the last prior to their fortieth year, even though they may live sixty years. Male potheads become sexually mature at about fourteen years, but are not socially mature until about seventeen years of age. Males are shorter-lived than females: out of 170 males examined by Kasuya and Marsh, the oldest was forty-six. The natural mortality of males is apparently higher than that of females at all ages.

Pilot whales are considered to be among the most social of the cetaceans, but little is known about the structure of their sociality. In the Pacific, these animals typically travel in groups or pods of between twenty and twenty-five, whereas in Newfoundland groups of a few hundred are quite common. Presumably the pod constitutes the basic social unit, and the larger groups are actually aggregations of several pods. The ratio of mature females to males in stranded, hunted, and free-ranging pods is always biased in favor of females, indicating polygyny. Researchers in Japan and Canada believe that the sex ratio is skewed because males suffer from a higher mortality rate than do females. Based upon the life history data collected on pilot whales killed in Japanese fisheries, researchers hypothesize that pilot whale pods are stable matrilineal kinship groups, in which females remain for life while males move to pods other than the one into which they are born. It remains unclear whether the pods actually have a single leader. Preliminary observations by one of us (Shane) suggest that pod composition may be stable over time.

Bonds between pilot whales, both in captivity and in the wild, appear to be very strong. An example of this attachment was demonstrated when a young adult female was caught by Marineland of the Pacific in Palos Verdes, California, and held on a line for five and one-half hours before being transported by boat. During her struggle, the whale was accompanied by five or six other pilot whales from her pod, as well as by several Pacific white-sided dolphins. The pilot whales swam just ahead of the captive and dove synchronously with her. The mother-calf bond is also very strong. Female pilot whales, like many other toothed cetaceans, will frequently carry their dead young for hours or days, both in captivity and in the wild. One of us (Shane) has discovered a unique variation on this behavior at Santa Catalina Island. There, pilot whales carry the bodies of dead California sea lions for hours or perhaps even days.

In contrast to the exuberant playfulness of most dolphins, pilot whale behavior is relatively sedate and single-minded. Aerial behaviors, such as leaping, are infrequent and probably have social connotations when they do occur. When feeding, these whales are found in dispersed herds usually composed of more than one pod. Because squid spawn on the bottom at depths of 50 to 120 feet in southern California, pilot whales are usually found within one-quarter to one mile of shore during the winter season. After feeding, the whales coalesce into distinct, well-organized pods, which travel parallel to the coast, possibly hunting for more food. The pods sometimes stop to rest, with each whale lying motionless at the surface and exposing only its melon and the leading edge of its dorsal fin. Resting pods frequently settle in a line-abreast formation. Sightings of small calves and the behavior of pilot whales in captivity suggest that mating may occur in the winter off southern California. In captivity, one element of courtship behavior involves violent head-butting in which the male and female slam their rounded melons into one another at high speed. Scarring is seen frequently on subadult males, indicating possible competition for status in a dominance hierarchy.

Pilot whales are often accompanied by other cetaceans and even by pinnipeds. Presumably pilot whale pods are exceptionally efficient at detecting food and so other marine mammals take advantage of this skill. The most common associate of pilot whales near the California Channel Islands is the bottlenose dolphin, but Pacific white-sided dolphins, common dolphins, and California sea lions are also seen with potheads.

Possibly the most perplexing behavior pattern of pilot whales and several other species is their tendency toward mass strandings, in which most whales usually die. In recent years, mass pilot whale strandings along the Pacific coast have occurred at Mazatlan and La Paz, Mexico, and on San Clemente Island off the coast of southern California, where twenty-eight animals swam ashore. So far, none of the many theories proposed to explain mass strandings has gained general acceptance. The popular concept of suicide seems unlikely, given our present knowledge about these and other cetaceans. The most prevalent theories among cetologists include the following. First, a combination of bottom or environmental conditions might render the animals' sonar ineffective. (This may be at least part of the explanation, as mass strandings occur in similar habitats, such as gently sloping beaches with sandy or muddy bottoms.) Second, heavy parasite infestations in the heads of the whales might render their sonar ineffective. Third, the pod leader for some reason might lose its sonar (from parasites?), or for some other reason swims onto a beach, and the pilot whales' strong social bond disposes the rest of the pod to follow. Fourth, the whales may be fleeing from killer whales or other danger, although this theory is less frequently considered.

Two more recent theories regarding strandings are of interest. Preliminary results of a comparison of live stranding localities and the contours of the earth's geomagnetic field suggest that these events often occur in areas where magnetic "valleys" intersect the coast. It has been suggested that the animals navigate in part by means of cues from the geomagnetic field and for some reason follow the "valleys" up to and onto the beach. Another theory suggests that strandings are a form of population regulation, occurring primarily in populations near their environmental carrying capacity, and most often in the core rather than at the peripheries of their ranges.

Like all cetaceans, pilot whales have efficient sonar on which they rely heavily for both navigation and prey location. Captive pilot whales have demonstrated that they can retrieve objects and swim efficiently in a tank with their eyes covered. Vision in these animals appears to be very good, although no experimental evidence is available on this point.

Pilot whales are highly auditory animals. They communicate primarily by vocalizations that include whistles and frequency modulated calls. Unlike dolphins, which vocalize at very high frequencies, most pilot whale sounds are below 15 kilohertz. Individual potheads probably have signature whistles, and vocalizations are more complex when these animals are highly aroused and interacting socially than when they are resting or traveling.

Pilot whale skin is sensitive and easily abraded. Physical contact may play an important role in communication. In captivity, pilot whales often respond favorably to touch and enjoy a brisk rubbing with a scrub brush. They are also easily trained in captivity and survive well. Often they form strong attachments to tank mates of different species.

Aside from the antics required for oceanarium performances, pilot whales have been trained for relatively complex maneuvers for a few research projects. In the United States Navy's "Project Deep Ops," a pilot whale was trained to work untethered in the open sea. There it learned to locate objects at depths of up to 1,650 feet by means of beepers. The animal carried a recovery device in his mouth and attached it to the located object, which was then raised by means of a gas generator and a lifting bag. Pilot whales trained in this manner could be used to help recover expensive oceanographic instruments or to carry out similar tasks.

The earliest record of a pilot whale fishery dates from the sixteenth century at the Faroe Islands, where a small, fairly stable yearly catch of around fifteen hundred whales continues to this day. The whales are captured by a "drive fishery" method whereby entire herds are driven ashore by villagers in rowboats and skiffs. Probably the largest drive fishery for these whales took place in Newfoundland between the mid-1940s and the mid-1960s, with catches approaching ten thousand whales during peak years. There is also a small fishery for the short-finned pilot whales at St. Vincent Island in the Caribbean, where two hundred or more whales were taken yearly by harpoon during the 1960s and 1970s. Recent catches, however, have decreased to fewer than twenty whales per year.

Aside from an undetermined number of harpoon catches by sperm whalers in the nineteenth and early twentieth centuries, there is no history of direct exploitation in the eastern Pacific. Some live captures have been made in this area for oceanariums and research facilities. In recent years, the pilot whales' pursuit of squid in the southern California Bight has resulted in direct competition with squid fishermen for the seasonally abundant cephalopods. Up to a dozen or more pilot whales have been killed there during winters when the squid fishery is in operation, most near Santa Catalina Island. The size of the whale population in this area is unknown, but from estimates of minimum numbers seen around Santa Catalina Island, the annual mortality may approach ten percent, constituting a potentially serious impact.

Although pilot whales lack the charisma and ebullience of most dolphin species, they are intriguing because of their tightly knit social groups and their persistent tendency toward mass stranding. The strong association between pilot whales and squid distribution, the disruption of these whales' normal patterns by El Niño, and their frequent association with other marine mammals indicate the important role these enigmatic cetaceans play in the marine ecosystem. Further long-term research holds the promise of unlocking some of the secrets surrounding the pilot whale.

8688

Skipjack Fisheries in the Western Atlantic

GARY T. SAKAGAWA

Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, California, 92038, U.S.A.

Available information on skipjack tuna in the western Atlantic Ocean is reviewed to identify areas where skipjack fisheries might be developed. Areas in the Gulf of Mexico, Caribbean Sea and off southeastern Brazil appear promising areas for development. Utilization of fish aggregating devices and new purse seining techniques are suggested as possible methods for concentrating schools and for catching them more efficiently.

L'information disponible sur le listao dans l'Atlantique ouest a été examinée pour définir les zones où il serait possible de développer la pêche de cette espèce. Des secteurs du golfe du Mexique, de la mer des Antilles et au large des côtes sud-est du Brésil semblent prometteurs à cet égard. L'emploi de dispositifs de concentration du poisson et de nouvelles modalités de pêche à la senne sont suggérés comme méthodes éventuelles de concentration des bancs et d'une pêche plus efficace de ces derniers.

Se estudia la información disponible sobre el listado del Atlántico Oeste con el fin de identificar aquellas zonas donde pudieran desarrollarse pesquerías de listado. Como más prometedoras parecen zonas en el Golfo de México, Mar Caribe y frente a la costa Sudeste del Brasil. Se sugiere la utilización de materias congregantes y técnicas de cerco como posibles métodos para concentrar los cardúmenes y capturarlos con mayor eficacia.

1. Introduction

A disproportionate amount of the total Atlantic catch of skipjack tuna (*Katsuwonus pelamis*) is taken in the eastern Atlantic. In 1981, 116,000 mt were caught in the eastern Atlantic whereas only 23,000 mt were caught in the western Atlantic. One reason is that fishing is more intense in the east than in the west. By fishing harder in the western Atlantic, can catches approach those from the east and if so, in what specific areas should the fishing effort be applied?

The first part of this question is answerable with a qualified yes: increasing fishing effort would probably increase catch. The second part concerning where this effort should be applied is the subject of this study. Data were drawn primarily from United States sources and from published documents; two unpublished documents (Rinaldo MS; Alverson and Verge MS) were used as secondary reference sources.

2. The Western Atlantic Region

The tropical and subtropical regions west of 30°W longitude are the western range of skipjack tuna in the Atlantic Ocean. The region includes waters off North and South America, the Gulf of Mexico and the Caribbean Sea. Within this region, environmental conditions, mainly the principal oceanic currents, seem to influence where skipjack tuna are concentrated and available for exploitation (see Evans et al. 1981).

For my analysis, I divided the region into four areas, corresponding roughly to the locations of the offshore ocean currents (Figure 1). Area A is north of the Florida Peninsula and west of 70°W longitude. In this area, the dominant ocean currents are the Florida Current and Gulf Stream. Area B includes the Gulf of Mexico, Caribbean Sea and waters east of the Antilles. The dominant ocean currents in this area are the Caribbean and Antilles currents. East of Area B (60°W longitude) is Area C, which extends southward to 5°S latitude. The dominant current in this area is the Equatorial Current. Area D is between 5°S and 40°S latitude and is characterized by the Brazil Current.

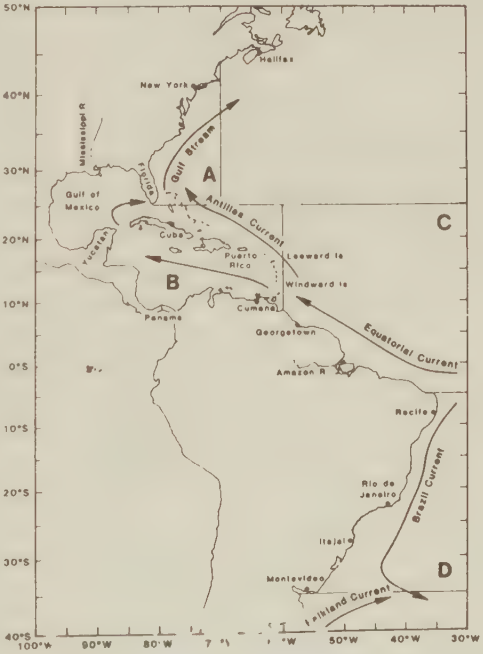


Figure 1. Four geographic areas of the western Atlantic used in the study. Locations of current skipjack tuna fisheries are shaded

2.1 Area A — North of the Florida Peninsula

Area A is not a productive skipjack tuna area for development of a major fishery. Exploration of the area for tunas was carried out in the 1940's and 1950's with baitboats, purse seiners, and longliners (Squire 1962; Wilson 1965). It was not until the late 1950's that a purse seine fishery for bluefin tuna (*Thunnus thynnus*) was established in Cape Cod Bay, U.S.A. and not until 1962 that this fishery expanded southward and began to also catch skipjack tuna. Catches of skipjack tuna have been small (<5,000 mt/yr) and variable from one year to the next (Sakagawa 1975). The catch is taken in the summer from a small area off New York and west of the Gulf Stream (Figure 1). The highest skipjack catch recorded for the fishery was 5,000 mt in 1964. In recent years, although the number of boats in the bluefin tuna fishery has remained steady (ICCAT 1982), and the bluefin catch reduced with quotas, the catch of skipjack tuna has not increased as the boats searched for alternative tuna species to fill their holds. The catch was 2,100 mt in 1981 and 200 mt in 1982.

Between the Florida Peninsula and New York (Figure 1), there is a large recreational fishery which takes skipjack tuna along with other species. The catch of skipjack tuna by this fishery is believed to be only a few tons annually (Deuel 1973). American tuna purse seiners have explored this region in the past, while traveling between the bluefin tuna fishing area and Puerto Rico. They have had little success in locating or catching skipjack tuna in this region.

2.2 Area B — Gulf of Mexico and Caribbean Sea

Besides scattered artisanal fisheries, Area B currently has two significant skipjack fisheries: one is a relatively small baitboat fishery along the northwestern and southwestern coast of Cuba (Suarez-Caabro y Duarte-Bello 1961; Carles and Hirtenfeld 1978), and the other is a baitboat and purse seine fishery off the northern and northeastern coast of Venezuela (Figure 1).

The year-round Cuban fishery has existed since the 1940's and currently produces an average of 2,000 mt/yr of mostly skipjack tuna together with a few tons of blackfin tuna (*T. atlanticus*). The skipjack tuna catch in 1982 was an estimated 1,300 mt.

The year-round Venezuelan fishery is a more recent development (Ramos y Gerardo-Guerra 1976). Established in about 1974 with baitboats only, it has expanded recently to include purse seiners. Information on this fishery is sketchy, but an estimated 4,900 mt of skipjack tuna were caught in 1981, and 14,000 mt in 1982 (ICCAT 1982a). The fishery catches both skipjack and yellowfin tunas.

Besides these two significant fishing areas, other sites in Area B have been explored for availability of tunas to capture with conventional tuna fishing gears. The best published accounts are by Wagner (1974) and Wagner and Wolf (1974). These authors describe results of exploratory fishing cruises conducted during 1967–70 between 10°N and 20°N latitude. Except in the Gulf of Honduras (15°–20°N latitude, 85°–88°W longitude), pelagic fish schools were seen in all areas surveyed, with the highest sighting rates around Puerto Rico (0.23 schools/hour) and in the Windward Islands (0.21 schools/hour). Small skipjack tuna schools (0.5–5 mt) were the most frequently encountered tuna schools. Pole-and-line catch rates were highest (32.8 kg of skipjack/hour) in the Windward Islands area. Troll catch rates were highest over the submerged banks of the northern Leeward Islands.

American tuna purse seiners that fish in the eastern tropical Atlantic survey Areas B and C for tuna schools while in transit between fishing areas and fishing ports. A typical route used by a purse seiner is from the eastern tropical Pacific fishing area through the Panama Canal and along the coast of South America to Puerto Rico for unloading or taking on fuel; then through the Windward Islands and along the coast of Trinidad, Guyana and Surinam, before heading eastward across the Atlantic to the fishing area off Africa. This same route is used on the return trip.

During such passages, fishing (and searching) for tunas are regular activities of the vessels. Data collected from vessel logbooks by National Marine Fisheries Service (NMFS) since 1966 were summarized by fishing effort (including searching effort), catch of skipjack tuna, and 1° square for location of effort (Table 1). Catches in Area B were primarily made off Venezuela, the Windward Islands and off the Mississippi River Delta (Figure 2). The amount of fishing

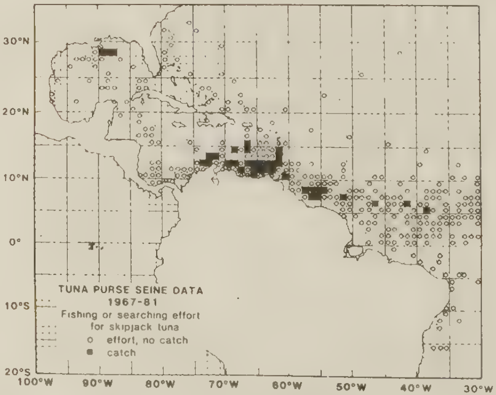


Figure 2. Location by 1° square of fishing effort and catches of skipjack tuna for American tropical tuna purse seiners that fished in the western Atlantic in 1967–81.

effort and catch for the fleet in any particular year was relatively small, but the aggregate total for the 15-year period is 1,493 days of fishing with 2,530 mt of skipjack tuna caught. The annual catch rates range from 0 to 5.31 mt/day's fishing, averaging 1.69 mt/day's fishing for the 15-year period. These yearly rates are almost always lower than those obtained by the American fleet in the eastern Atlantic (2.2–17.0 mt/day's fishing).

Table 1. Summary of catch and effort data for American tuna purse seiners that fished in the western tropical Atlantic Ocean.

Year	Months	Fishing effort (days)	Catch (mt)	Catch rate (mt/day)
1967	Aug, Sep, Oct	13	0	0
1968	Jul, Oct–Dec	43	0	0
1969	Nov	1	0	0
1970	Jul, Aug, Oct	3	0	0
1971	Jun	3	0	0
1972	May–Aug, Nov	79	7	0.09
1973	May–Aug	10	0	0
1974	Jul, Nov	20	0	0
1975	Mar, Jun–Dec	106	52	0.49
1976	Mar–Jun, Aug, Sep, Nov	104	552	5.31
1977	Jan, Apr–Jun, Aug, Sep, Nov	89	24	0.27
1978	Jan–Nov	427	1146	2.68
1979	May, Jun, Aug–Oct	150	299	1.99
1980	Apr, May, Nov, Dec	49	0	0
1981	Jan–Oct	396	450	1.14
Total		1493	2530	1.69

During 1950–69, the Bureau of Commercial Fisheries, predecessor of NMFS, sponsored a number of exploratory finfish and shrimp surveys primarily with research vessels in Area B. Normal survey procedures included trolling of several lines, searching for pelagic fish schools and recording general information on the behavior of the schools. I tabulated all reported sightings that were recorded as skipjack tuna schools, which in reality probably consisted occasionally of other tuna species as well, by 1° square for sighting location. The majority of these schools sighted were reported to be "moving fast" or "subsurface" (swimming deep). The results (Figure 3) show clusters of sightings off the Mississippi River delta, around the Florida Peninsula, off Cuba and in the Leeward and Windward Islands.

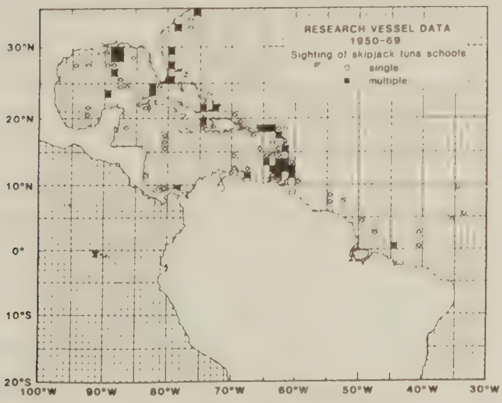


Figure 3. Location by 1° square of sightings of skipjack tuna schools. Data from National Marine Fisheries Service research vessel cruises for the period 1950–69.

In 1980 NMFS executed a special skipjack tagging cruise in the eastern part of Area B with the commercial baitboat, *Rhonda Sue* (Rinaldo et al. 1981). A total of 143 pelagic fish schools were sighted during approximately forty-three days of searching. Skipjack tuna was the primary species in fifty-three of the schools sighted. Assuming a ten-hour searching day, the sighting rates were 0.33 pelagic fish schools/hour and 0.12 skipjack schools/hour. Most sightings were in the Leeward and Windward Islands and to the east and southeast of Trinidad (Figure 4). Most of the schools were reported to be difficult to fish because they were moving at high speed.

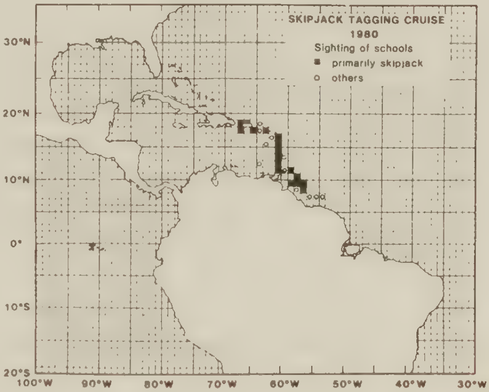


Figure 4. Location by 1° square of sightings of pelagic fish schools made during a National Marine Fisheries Service skipjack tagging cruise with a commercial baitboat in 1980.

These results indicate that Area B still has potential sites for development of skipjack fisheries. Off the Mississippi River Delta and off the west coast of the Leeward and Windward Islands are likely sites, although the density of schools appears at first glance to be too low to sustain purse seining operations. For example, in the Leeward and Windward Islands the sighting rates are about two to three schools per day of searching, assuming ten hours of searching in a day. A purse seiner is capable of setting on two to five schools per day, but when searching time is taken into account, this rate is lower. For the American purse seine fleet, the rate has been 0.6–1.7 sets/day's fishing in the eastern tropical Atlantic during 1966–80. Thus, the sighting rate of two to three schools per day of searching appears capable of sustaining purse seining operations.

The schools in Area B are generally described as being "wild", difficult to fish with pole-and-line or purse seiners, and relatively small in size. This school characteristic might have discouraged development of large-scale skipjack fisheries in Area B so far. The introduction of new fishing techniques such as the use of fish aggregating devices (Matsumoto et al. 1981; Kihara 1981) and lighter and larger purse seine nets, which have been successfully used in the western Pacific Ocean (Anon. 1976), might be the solution. Aggregating devices are particularly appropriate because they are easy to construct and deploy in locations within reach of local fishermen.

2.3 Area C — Off Venezuela to Brazil

Area C (Figure 1) currently has a developing baitboat and purse seine fishery. Information on this fishery is limited, but it is believed that the area of operation is from southeast of Trinidad to off Georgetown, Guyana. According to Calderón de Vizcaino and Salazar (1984), Venezuelan baitboats are involved in this fishery and in 1981, the Venezuelan baitboats landed approximately 48,500 skipjack tuna and 10 yellowfin tuna (*T. albacares*).

Exploratory fishing data (Wagner 1974; Rinaldo et al. 1981) for this area indicate that school density is low, and the schools generally move at high speed. It seems, therefore, that sustained high production by this fishery will depend on the adoption of new fishing techniques.

South of Georgetown, there has been little searching effort for skipjack tuna. Data from logbooks of American purse seiners indicate a low success rate in catching skipjack tuna (Figure 2). All of the catches were in a band between 5°N and 10°N latitude, or in the Inter-tropical Convergence Zone (Evans et al. 1981). This area receives strong northeasterly tradewinds especially during October through March. Fishermen claim that these winds prevent effective searching and fishing for tunas and this alone makes it unlikely, barring technological innovation, that a major fishery will develop.

2.4 Area D — Off Brazil

The potential skipjack fishing zone in Area D is bounded by the Brazilian coast and the Brazil Current (Evans et al. 1981). So far only the southern region of this zone, from Rio de Janeiro to about Itajai, has been developed (Figure 1). The year-round baitboat fishery, started in 1979, produced 13,900 mt in 1981 and an estimated 17,000 mt in 1982 (Negreiros and Meneses de Lima 1980; ICCAT 1982a). The fishery is limited to a narrow band along the coast where current studies indicate skipjack are most readily available to surface gears (Evans et al. 1981; Maluf et al. 1984).

North of Rio de Janeiro, surveys for tropical tunas sponsored by primarily Brazilian interests have been made, but results of the surveys have not been made public. Judging from information on the oceanography of the region (Zavala-Camin 1978; Evans et al. 1981; Matsuura 1982a), however, this area looks promising for development of a skipjack tuna fishery.

3. Discussion

Skipjack tuna are taken by a range of surface fisheries, from artisanal to large-scale, in the western Atlantic. The current catch from the region is only sixteen percent of the total skipjack tuna catch of the Atlantic Ocean. By increasing fishing effort in selected areas of the region, it is possible to increase the catch.

Available data primarily from United States sources were reviewed to identify promising areas for further skipjack fishery development in the western Atlantic. These data provided the basis for a number of tentative conclusions: (1) the area north of the Florida Peninsula (Area A) does not appear to be capable of supporting a sustained commercial skipjack fishery. Availability of large concentrations of fish is variable from one year to another, probably influenced by environmental conditions such as favorable temperature and oxygen levels, availability of food supply and perhaps the presence of cold-core rings (The Ring Group 1981). (2) The Gulf of Mexico and Caribbean Sea (Area B) appear to have promise for expanding existing or developing new skipjack tuna fisheries. However, progress will depend on the introduction of new fishing techniques for more effective interception of the fast moving schools and for concentrating the relatively small schools. Fish aggregating devices and large, light-weight purse seine nets are new techniques that might aid development. (3) With the exception of an area southeast of Trinidad, the area south of Georgetown, Guyana to about Recife, Brazil does not appear to have much promise for skipjack fishery development. The severe weather seems to be the limiting factor. The area southeast of Trinidad has a developing fishery; growth of this fishery can be improved with introduction of new fishing techniques. (4) The area south of Recife to about Itajai, Brazil (Area D) appears to have promise for further development. However, actual fishing survey information is needed for a part of the area between Recife and Rio de Janeiro before a full evaluation of the area's potential can be made.

Acknowledgement

Grant Beardsley, Atilio Coan and Ronald Rinaldo assisted in identifying and locating data for this study. I also acknowledge the contribution of participants of the International Skipjack Year Program, who shared information on the developing fisheries and helped to sharpen my thinking and conclusions on tuna fisheries potential in the Atlantic Ocean.

Some Recent Changes in the Atlantic Skipjack Tuna Fishery

G. Sakagawa and A. Coan

Southwest Fisheries Center, P.O. Box 271, La Jolla, CA. 92038, U.S.A.

ICCAT's International Skipjack Year Program was instrumental in drawing attention to the presence of the underutilized resource of skipjack Tuna (*Katsuwonus pelamis*) in the Atlantic Ocean and in encouraging increased exploration and exploitation of the resource. Comparison of fisheries statistics for the period before 1979 and from 1979 and afterwards, when the four-year program was in effect, demonstrates that the fisheries for skipjack tuna have undergone expansion and changes. The Atlantic catch of skipjack tuna, for example, increased from an average of 91,300 MT in 1975–78 to an average of 118,300 MT in 1979–82.

Le Programme de l'Année internationale du Listao de l'ICCAT a été déterminant pour attirer l'attention sur la présence de ressources sous-exploitées de listao (*Katsuwonus pelamis*) dans l'Atlantique et stimuler une exploration et exploitation plus poussées de ces stocks. La comparaison des statistiques de pêche pour la période antérieure et postérieure à 1979, date à laquelle le programme est entré en vigueur, démontre que les pêcheries de listao ont subi une expansion et des modifications, les prises de listaos dans l'Atlantique, par exemple, ont augumenté, d'une moyenne de 91.300 TM en 1975–78 à une moyenne de 118.300 TM en 1979–82.

El Programa del Año Internacional Listado de ICCAT ha contribuído a llamar la atención sobre la existencia del recurso infrautilizado del listado (*Katsuwonus pelamis* en el Océano Atlántico, y a estimular una mayor exploración y explotación del recurso. La comparación de las estadísticas de pesquerias para el periodo anterior a 1979 y desde 1979 en adelante, cuando el programa de cuatro años de duración estaba en vigor, demuestra que las pesquerias de listado han experimentado expansión y cambios. La captura de listado del Atlántico, por ejemplo, aumentó de un promedio de 91.300 TM en 1975–78 a un promedio de 118.300 TM en 1979–82.

8689

PREY SIZE SELECTIVITY AND FEEDING RATE OF LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX* GIRARD

PATRICIA D. SCHMITT
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

A series of laboratory feeding experiments was conducted with larvae of the northern anchovy, *Engraulis mordax*, at 10, 20, 30, and 40 mm SL. The larvae were fed wild zooplankton in high (100 prey/liter) and low (10 prey/liter) concentrations. The 10-mm larvae consumed primarily rotifers, probably because of their past feeding history. The 20-40-mm larvae tended to select large copepods at high concentrations, and medium and large copepods at low concentrations. The ability of late larvae to select the largest prey available is similar to the foraging behavior of adult anchovies reported by previous workers. The foraging of 40-mm larvae was probably restricted by the size of the experimental tanks.

Feeding rates as a function of larval size and prey concentration were estimated and compared to a conservative estimate of basal metabolic costs. Only 20- and 30-mm larvae feeding at 100 prey/liter consumed enough food to grow at rates similar to those observed in the sea, which indicates that even late larvae require somewhat concentrated patches of food.

RESUMEN

Una serie de experimentos de alimentación en laboratorio se llevó a cabo con larvas de anchoveta del norte, *Engraulis mordax*, de 10, 20, 30, y 40 mm (largo estándar). Las larvas fueron alimentadas con concentraciones altas (100 presas/litro) y bajas (10 presas/litro) de zooplancton silvestre. Las larvas de 10 mm consumieron principalmente rotíferos, probablemente debido a su historial de alimentación previo. Las larvas de 20 a 40 mm LS seleccionaron principalmente copépodos grandes a altas concentraciones, y copépodos medianos y grandes a concentraciones bajas. La habilidad de las larvas maduras para escoger las presas disponibles más grandes es similar al comportamiento depredador de las anchovetas adultas de acuerdo a lo informado por otros investigadores. La predación de las larvas de 40 mm probablemente fue restringida por el tamaño del tanque experimental.

Las tasas de alimentación fueron calculadas como función del tamaño larvario y de la concentración de presas y fueron comparadas con una estimación de los costos en metabolismo basal. Sólo las larvas de 20 a 30 mm, quienes consumieron 100 presas por litro, se alimentaron lo suficiente como para crecer a tasas similares a las observadas en el mar. Esto indica que incluso las larvas maduras requieren la presencia de sus presas concentradas en "manchas."

INTRODUCTION

In order to understand the factors affecting recruitment and year-class strength, scientists have done much research on the early life history of the northern anchovy, *Engraulis mordax* Girard. The rationale behind this work has been that year-class strength may be determined by the growth and mortality rates of larvae in the first month of life (5-15 mm SL), especially during the transition from the yolk-sac stage to planktivorous feeding (Lasker 1975). However, correlation of the densities of early larvae (less than 15 mm SL) with the strength of the subsequent year class has shown that only exceptionally small recruitment can be predicted, not medium or large recruitment (Smith 1981). Smith and Lasker (1978) note that an increase of an order of magnitude occurred in the anchovy population between 1951 and 1969, while the annual average daily production of 20-day-old larvae remained relatively constant. From this observation it is apparent that variations in survival during the late larval phase (20-35 mm SL, ca. 1-3 months old) are also important in determining recruitment (Smith 1985). The late larval and juvenile stages are presently the least understood phases of *E. mordax*.

Feeding and growth characteristics of northern anchovy show gradual changes from early to late larval stages. Northern anchovy larvae of all sizes feed by visually mediated biting (Blaxter and Hunter 1982). Filter feeding begins only after metamorphosis (35-40 mm SL). As a larva grows, it requires more food of a larger size to maintain a given rate of growth. However, there seems to be no further increase in food size after larvae reach about 12 mm SL, even though the mouth width, and therefore the size of particles ingestible, continues to increase (Hunter 1981). In the field, there are far more food particles of the size taken by first-feeding larvae (50-100 μm) than there are of larger particles needed by older larvae (ca. 200 μm and larger) (Arthur 1977; Hunter 1981). The maximum

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naupliar biomass in waters of the California Current occurs at a naupliar width of about 70 μm (Arthur 1977). Measurements of the standing stocks of pelagic organisms indicate that there is approximately equal biomass over logarithmically equal size ranges (Sheldon et al. 1977); in other words, the number of organisms decreases exponentially as size of organisms increases linearly (Vlymen 1977).

Jack mackerel larvae inhabiting the same general environment as the anchovy are able to secure increasingly larger food particles as they grow (Arthur 1976). This suggests that factors other than mouth size, such as the relatively slow swimming speed of engrauliid larvae, may limit the size of food captured by *E. mordax* (Hunter 1981). Late larvae are thought to continue to feed on smaller prey and to take larger copepods when available, although this apparently has not been examined in either field-caught or laboratory-reared larvae larger than 20 mm SL (Arthur 1976; Hunter 1981).

Methot (1981) reports that late larvae grow at a slower rate (0.30-0.35 mm/day) than early larvae (0.47-0.70 mm/day) or early juveniles (0.40-0.60 mm/day). The ratio between weight and length seems similar during all stages (Methot 1981); therefore, the reason for slower length-specific growth during the late larval stage may lie in feeding ecology, energetic requirements, and assimilation efficiency. Methot (1981) suggests that the decline in growth through the late larval period may be due to the inability of larvae to find and capture large particles.

Here I present the results of laboratory experiments conducted with *E. mordax* larvae fed wild zooplankton to determine how prey-size selectivity and feeding rates differ between larvae of various sizes that are feeding on different densities of prey. The results are used to infer whether larvae can obtain enough food at the experimental prey concentrations to meet metabolic and growth requirements.

METHODS

Larvae of *Engraulis mordax* were reared from eggs at 18°C in the laboratory at the Southwest Fisheries Center, La Jolla, California, using the methods presented by Hunter (1976). Larvae were fed the dinoflagellate *Gymnodinium splendens*, the rotifer *Brachionus plicatilis*, and the harpacticoid copepod *Tigriopus californicus*, all reared in the laboratory.

Wild zooplankton for the feeding experiments was collected in Mission Bay from October 25, 1984, to February 21, 1985. Collections were made from a skiff, with 0.5-m ring nets of 64-μm and 333-μm nylon mesh. The nets were fitted with solid cod ends. The two nets were towed sequentially for 5 minutes each at approximately 1 m/sec, and the catches from six sets of tows were combined. The most abundant organisms collected were calanoid copepods of the genus *Acartia*. Also common were the cyclopoid copepods *Corycaeus* spp. and *Oithona* spp., and the harpacticoid copepod *Euterpina acutifrons*. Gastropod veligers and rotifers were occasionally abundant.

Experimental Design

The experimental design was orthogonal, with two main factors—larval length (10, 20, 30, and 40 mm SL) and prey concentration (10/liter and 100/liter). The larval lengths were chosen to cover the entire larval life in this species. The prey concentrations were chosen to approximate high and low average densities of microzooplankton prey sampled in areas inhabited by anchovy larvae in the California Current (Arthur 1977). Each combination of factors and levels was replicated twice. Only two tanks were available for experiments; therefore, experiments with the two prey concentrations were done simultaneously for a particular size of fish. The size-composition of wild plankton varied between experiments because of natural variations in the plankton collections. The order of experiments was randomized so that any seasonal change in plankton composition was interspersed among sizes of larvae.

Experimental Procedure

One to three days before an experiment, I transferred 20-30 reared larvae to each experimental tank. The experimental tanks were as similar as possible to the rearing tanks in construction (400-liter, 1.2-m-diameter, black fiberglass), aeration, lighting, and temperature. Larvae were starved and acclimated for 1-3 days, depending on size, until guts were empty and behavior seemed normal.

Fresh plankton was collected each morning (0800-1200 hrs), and experiments were conducted in the afternoon (1400-1800 hrs). Immediately before the experiment, I stopped the aeration. I then added the appropriate amount of plankton to create the target concentration. To determine the actual concentration and distribution of prey in each tank, I took samples with plexiglas tubes (7-cm diameter) lowered onto rubber stoppers that had been placed on the bottom before I added plankton. Sample volume ranged from 500-750 ml, depending on the volume of water in the tank. I preserved five replicate samples in 5% buffered Formalin for later enumeration. I used size-frequency data from samples in the high-density tank (100/liter) to determine size-frequency in the low-density tank (10/liter). Pilot studies indicated a coefficient of variation between replicate samples of 8%-74%.

I measured swimming speed for two 10-minute periods before and after plankton was added. To measure the speed, I randomly selected an individual fish, and then, with the aid of 1-cm and 3-cm grid patterns on the bottom of the tank, estimated the distance the fish traveled in 2 seconds. The number of fish observed in 10 minutes ranged from 35 to 142. I converted speeds into body lengths/sec, using the mean standard length of the fish in each tank.

I terminated the experiments after 30-60 minutes by anesthetizing all fish with MS_{222}, at a concentration of 0.1 g/l. This was done to prevent the larvae from defecating or regurgitating their gut contents during handling (June and Carlson 1971). After 10 minutes, I collected fish with a dip net as quickly as possible, and preserved them in 10% buffered Formalin for later measurement and enumeration of gut contents. Duration of the experiments was assumed to be less than the time required for larvae to fill their guts at the experimental prey concentrations or to defecate prey ingested during the experiment (G. Theilacker, pers. comm.).

Laboratory Analyses

All prey items were identified in three categories: nauplii, copepods (including copepodites and adult copepods), and others. I measured items across the maximum width, excluding appendages. Initially I grouped the measurements into 50-μm size categories, and later regrouped them into five categories for data analysis: nauplii (< 150 μm wide), small copepods (< 100 μm wide), medium copepods (100-300 μm wide), large copepods (> 300 μm wide), and others (predominantly rotifers < 200 μm; also gastropod and bivalve veligers).

Plankton samples were stained with Biebrich scarlet, and counted in either a settling chamber with an inverted microscope at 50-100×, or a Plexiglas counting dish under a dissecting microscope at 25-50×. In the settling chamber, some plankters were found in the supernatant after the settling period of 12-15 hr. I estimated the percentage of error (i.e., the proportion of plankters not settling completely) from 20 samples; it averaged 15.1% for nauplii and copepods. There was no significant size-bias in the error factor. All counts made with settling columns were subsequently corrected.

I examined the guts of ten larvae from each experiment (except for one experiment with 10-mm larvae, when only eight larvae were available). I measured the fish (SL), and dissected the guts in glycerin. I teased out the gut contents with fine needles, and stained them with Chlorazol Black E in lactic acid and ethyl alcohol (Judkins and Fleminger 1972). All prey items were counted and measured under a compound microscope.

I determined the live length of each fish by using the shrinkage correction factors of Theilacker (1980) for 10 min of net treatment followed by preservation in 10% Formalin. Shrinkage rates due to MS_{222} and net treatment were similar. For 10-mm larvae, the shrinkage from 10 min in 0.1 g/l MS_{222} followed by Formalin preservation was 13.1% ($n = 20$), compared to 15% from 10 min of net treatment followed by Formalin preservation (Theilacker 1980).

Gut contents and plankton data were converted from numbers of prey to dry weight, taking into account the size-frequency of prey by 50-μm width classes before the data were combined into the five larger prey classes for analysis. The width-specific volumes of copepods and nauplii were calculated from ocular micrometer measurements of the length, width, and depth, assuming nauplii to be ellipsoids, and copepods to be ellipsoids (cephalothorax) plus cylinders (abdomen). I determined volume-to-width relationships for nauplii [ln volume = $-14.20 + 3.08$ (ln width), $r^2 = 0.902$, $n = 42$] and copepods [ln volume = $-13.56 + 3.02$ (ln width, $r^2 = 0.993$, $n = 75$]. The width-specific dry weight of fresh, mixed-species copepod samples was determined following the methods of Theilacker and Kimball (1984). I rinsed samples with isotonic ammonium formate solution (3.4%), sorted them into 50-μm size classes, and dried them overnight on glass slides at 60°C. I prepared 14 slides, each containing from 3 to 95 individuals, depending on the size of copepods. Following drying, samples were removed from the slides and weighed on a Cahn electrobalance. I determined the dry-weight-to-volume relationship by linear regression with intercept set equal to 0 [dry weight = 0.19 (volume), $p < .001$, $n = 14$], and used the relationship to calculate dry weights of nauplii and copepods from their volume. The dry weight used for the prey category "others" was the average for rotifers < 200 μm wide (0.30 μg) given by Theilacker and Kimball (1984).

Data Analyses

Prey-size selectivity was determined using the alpha index (α) (Chesson 1978). I chose this index because it allows comparisons of selectivity between experiments with different prey compositions (Chesson 1983), and also because it is possible to test the apparent selectivity against a random model (Manly 1974). The index is calculated as:

$$\alpha_i = \frac{r_i/p_i}{\sum\limits_{i=1}^{m} r_i/p_i}$$

where m = number of prey types = 5
r_i = proportion of prey type i consumed
p_i = proportion of prey type i available.

p_i was assumed to be constant for the duration of each experiment; i.e., the initial prey concentration was assumed to be not significantly depleted by larvae feeding during the experiment. r_i was determined from gut content analyses.

I calculated the alpha index for each of the five prey categories, for each larva that fed during experiments. The values so obtained were not suitable for parametric statistical analyses, because the variances remained heterogeneous after arc sine transformation. Therefore, I examined the median values and the quartiles above and below the median. The observed values are compared with the value expected if feeding was random on all categories of prey ($\alpha = 1/m = 0.20$).

In order to compare feeding rates between sizes of larvae at the target concentrations, I fitted feeding-rate data for each 10-mm size class of larvae to a log-linear multiple regression model:

$$\ln(\text{rate} + 1) = \ln(a) + b_1(\text{SL}) + b_2(\text{concentration})$$

I backtransformed the resulting estimates, taking into account the variance of the regression, and calculated 95% confidence limits (Beauchamp and Olson 1973).

I calculated the metabolic and growth requirements using the following values and assumptions:

1. Larvae fed at the estimated mean feeding rates throughout a 12-hr feeding day.

2. Daily minimum metabolic requirement (24 hr) was calculated from the following model presented by Theilacker[1] for anchovy larvae at 15.5°-16°C:

$$Q = 4.269\, W^{0.697}$$

where Q = metabolic rate in μl O_2/day
W = fresh dry weight in mg

and converted to μg prey material using the following factors: 0.00463 cal/μl O_2 and 4.9×10^{-3} cal/μg, for copepod prey (Theilacker and Kimball 1984).

3. Assimilation efficiency was 70% for larvae of all sizes, a rough extrapolation from Theilacker's results.[2]

4. Weight-specific growth rates of larvae in the sea were taken from Methot (1981). The surface temperatures reported in that study (generally representative of anchovy spawning areas) ranged from 13° to 19°C, with the mode at approximately 15°-16°C.

5. Fresh dry weights were calculated from the formula in Hunter (1976) for 10-30-mm larvae, and from unpublished data of Hunter for 40-mm larvae.

RESULTS AND DISCUSSION

The target and actual larval lengths and prey concentrations are given in Table 1, along with the feeding incidence (% of larvae with one or more prey in gut). Because 10-mm larvae did not feed at 10 prey/liter, I tested them at 100 and 1000 prey/liter. Feeding incidence tended to increase with both larval length and prey concentration; similar results have been reported for other species of fish larvae (Houde and Schekter 1980).

Swimming Activity

The mean swimming speed, measured as body lengths/sec (bl/s), in each experiment is shown in Table 2, along with t-tests of the equality of means before feeding (after 1-3 days of food deprivation) and during feeding. For 10-mm larvae, mean speed was always less than 1 bl/s, and showed no changes with the addition of food. My results contrast with those of a previous study in which anchovy larvae from 4-8 days old (< 6 mm SL) swam slower when inside a dense patch of food cells (up to 260 cells/ml) than when outside such a patch (Hunter and Thomas 1974). The difference in these results could be because the "patches" created by adding food in my experiments were 3 to 4 orders of magnitude less dense than those used by Hunter and Thomas.

For 20-40-mm larvae, mean swimming speed ranged from 0.6 to 3.3 bl/s and tended to increase during feeding (9 of 11 t-tests with $p < .10$). However, there was no difference in the relative increase in speed during feeding between high and low prey concentrations; i.e., larvae did not swim faster while feeding on high prey concentrations (Table 2).

Prey Selectivity

The mean proportion of various prey types consumed by various sizes of larvae at high and low concentrations is compared to the mean available size composition in Figure 1. The 10-mm larvae consumed primarily rotifers (the "others" category), although they consumed some nauplii and copepods at 1000 prey/liter. The 20-40-mm larvae tended to consume a higher proportion of nauplii at low concentrations than at high concentrations, and higher proportions of medium and large copepods at high concentrations than at low concentrations. Medium copepods (100-300 μm wide) formed the largest proportion (50%-80%) of prey consumed, both by numbers and by weight for 20-40-mm larvae at both concentrations.

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[1] Theilacker, G.H. MS. Feeding ecology and growth energetics of larval northern anchovy, *Engraulis mordax*

[2] Ibid

TABLE 1
Comparison of Target Values for Standard Length of Northern Anchovy Larvae and Prey Concentrations with the Mean Values for Two Experiments

Target		Actual			
SL (mm)	Conc. (no./liter)	SL (mm)	Conc. (no./liter)	Conc. (µg./liter)	Feeding incidence (%)
10	100	10.2 (1.8)	278.1 (61.0)	148.1 (25.5)	77.8
	1,000		1,173.0 (148.8)	969.2 (53.6)	72.2
20	10	22.2 (2.2)	36.9 (16.4)	23.6 (13.2)	50.0
	100		92.2 (19.8)	64.6 (10.5)	95.0
30	10	28.4 (3.0)	19.5 (9.5)	9.0 (3.7)	85.0
	100		127.3 (18.7)	92.9 (42.7)	100.0
40	10	43.0 (5.0)	10.2 (0.4)	7.9 (4.3)	100.0
	100		166.0 (58.5)	264.9 (165.9)	100.0

Standard deviation is shown in parentheses below mean values.

TABLE 2
Mean Swimming Speed (Body Lengths/Sec) of Northern Anchovy Larvae Before and During Feeding Experiments, and Results of t-Tests of the Equality of Means

		Swimming speed (body lengths/sec)			
SL (mm)	Prey conc.	Before	During	t	p
10	Low	0.8 (0.3)	0.8 (0.3)	0	ns
	High	0.8 (0.3)	0.7 (0.3)	1.5	>.10
	High	0.5 (0.4)	0.5 (0.4)	0	ns
	Low	0.7 (0.4)	0.7 (0.4)	0	ns
20	Low	0.6 (0.4)	1.8 (1.2)	−10.2	<.001
	High	1.3 (1.2)	2.0 (0.9)	−5.2	<.001
	Low	1.2 (0.6)	2.3 (1.1)	−6.9	<.001
	High	1.5 (1.2)	1.9 (1.1)	−1.9	<.10
30	Low	2.6 (1.2)	3.0 (1.4)	−1.8	<.10
	High	3.3 (0.9)	2.2 (0.7)	8.7	<.001
	Low	2.3 (1.1)	2.1 (0.8)	−1.2	>.20
	High	1.3 (0.6)	1.6 (0.6)	−2.9	<.001
40	Low	1.4 (0.8)	1.6 (0.6)	−1.8	<.10
	High	1.2 (0.5)	1.9 (0.5)	−9.1	<.001
	High	1.0 (0.4)	2.7 (0.6)	−18.2	<.001

Standard deviation is shown in parentheses after each mean. The number of observations for each mean ranged from 35 to 142.

The alpha indexes of selectivity are presented in Figure 2, and compared to the random feeding value of 0.20. The 10-mm larvae were highly selective for rotifers. This could have been influenced by two factors. First, there was a large proportion of rotifers in the tank during the experiment. The rotifers came both from the plankton used for the experiment (collected by chance during a rotifer bloom) and from the rearing tanks when the fish were transferred. Before the experiments began, I attempted to remove the transferred rotifers using an air-lift pump, but was not entirely successful. The second factor was the larvae's lack of experience with wild zooplankton as food. The 10-mm larvae were accustomed to eating cultured rotifers, and may have been unable to adjust to wild plankton in the time allowed by the experiment. However, in the field, anchovy larvae select prey smaller than the largest they are capable of ingesting (Arthur 1976). In the laboratory, herring larvae (12-19 mm SL) selected wild zooplankton narrower than the widest available and ingestible during feeding experiments, even though they were accustomed to wild zooplankton as food during rearing (Checkley 1982). The fact that 10-mm anchovies ate more medium copepods at 1000/liter than at 100/liter suggests that they were better able to capture

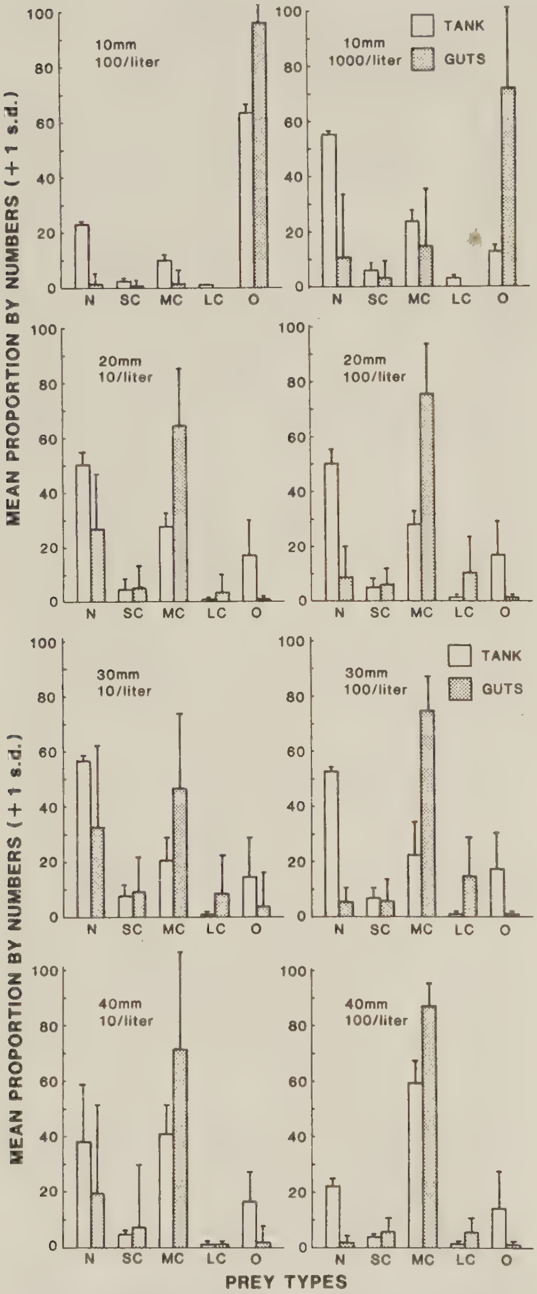

Figure 1. Comparisons of the proportions of various prey types consumed versus the proportions available to northern anchovy larvae of 10, 20, 30, and 40 mm SL, feeding at high and low prey concentrations. Mean values for two experiments are indicated by bars, with 1 standard deviation shown by a line above each bar. Prey types are abbreviated as follows: N, nauplii < 150 μm wide; SC, small copepods < 100 μm wide; MC, medium copepods 100-300 μm wide; LC, large copepods > 300 μm wide; and O, others (mainly rotifers < 200 μm wide, and gastropod and bivalve veligers)

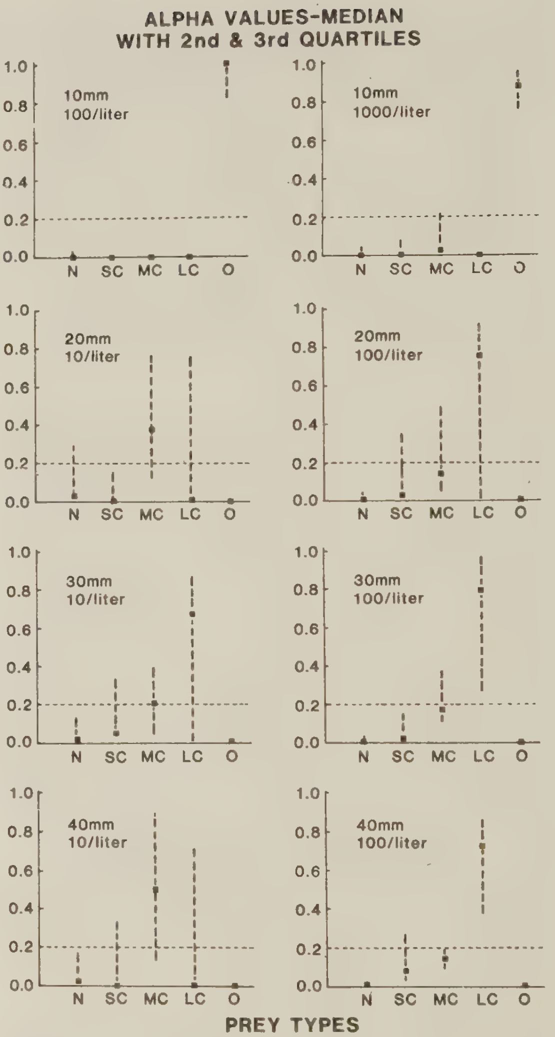

Figure 2. Values of the alpha index of selectivity for each prey type, size of northern anchovy larvae, and prey concentration. The median value from two experiments (number of fish = 20) is shown by the square symbol, with the quartiles above and below the median indicated by the vertical dashed lines. The random feeding value ($\alpha = 0.20$) is shown by the horizontal dashed line on each graph. The prey types are abbreviated as in Figure 1.

larger prey at high density, regardless of previous experience. The larger larvae (20-40 mm) had all been previously exposed to wild plankton as an occasional food source in the rearing tanks.

The 20-40-mm larvae tended to select large copepods at high concentrations, and to select medium and large copepods at low concentrations. There is obviously much individual variation in selectivity. No clear pattern of difference in selectivity or size composition of prey consumed appears to exist between 20-, 30-, and 40-mm larvae; all tended to select the largest prey available. Adult northern anchovy in the Southern California Bight showed similar selectivity for the largest prey available while feeding in schools on a variety of plankton assemblages of prey genera and sizes overlapping those used here (Koslow 1981).

There was some indication that the 20-40-mm larvae may have significantly reduced the concentration of larger prey during some experiments, but this depletion was not quantified. Such a violation of the assumption of constant p_i would tend to make the alpha values presented here an underestimation of the actual degree of selectivity (Chesson 1978, 1983; Manly 1974).

Feeding Rates

Estimated feeding rates (Figure 3), given both as numbers per minute and as dry weight per minute, were calculated from multiple regression equations describing feeding rate as a function of larval size and prey concentration for each 10-mm size class (Table 3). Feeding rate was higher at 100/liter than at 10/liter for all sizes of larvae. At 100 prey/liter, 40-mm larvae consumed 1.5-2 times more items than did 20- and 30-mm larvae. However, in terms of dry weight of prey consumed/min, 40-mm larvae consumed less than did 30-mm larvae, indicating that 40-mm larvae ate more small prey than did 30-mm larvae. This may be because the experimental tank was small relative to the searching abilities of 40-mm larvae, and because 40-mm larvae apparently depleted the tank of large copepods during the experiment.

Metabolic and Growth Requirements

The results of the calculations of food consumed and metabolic costs are presented in Table 4. For all sizes of larvae at all concentrations (except 20-mm larvae at 10/liter), larvae ingested enough food to meet their basal metabolic needs. However, the consumption rates used here are probably somewhat high for two reasons: (1) feeding rates were measured during the first 30-60 minutes of feeding after a period of starvation, and were thus higher than an average 12-hour rate (Hunter 1972); and (2) feeding rates were measured at 18°C, whereas minimum metabolic requirements and field growth rates are more representative of larvae at 15°-16°C.

Nevertheless, estimated growth rates as a percentage of body weight are compared with the weight-specific growth rates of field-caught larvae (Methot 1981) to determine if larvae could grow at observed rates at the prey concentrations tested (Table 4). Neither 10-mm nor 40-mm larvae could grow at field growth rates at any of the food concentrations tested, but I do not believe the results for these two size classes are reliable. The feeding of 10-mm larvae was probably not typical, because prior feeding was only on rotifers. Foraging of 40-mm larvae was probably affected by tank size.

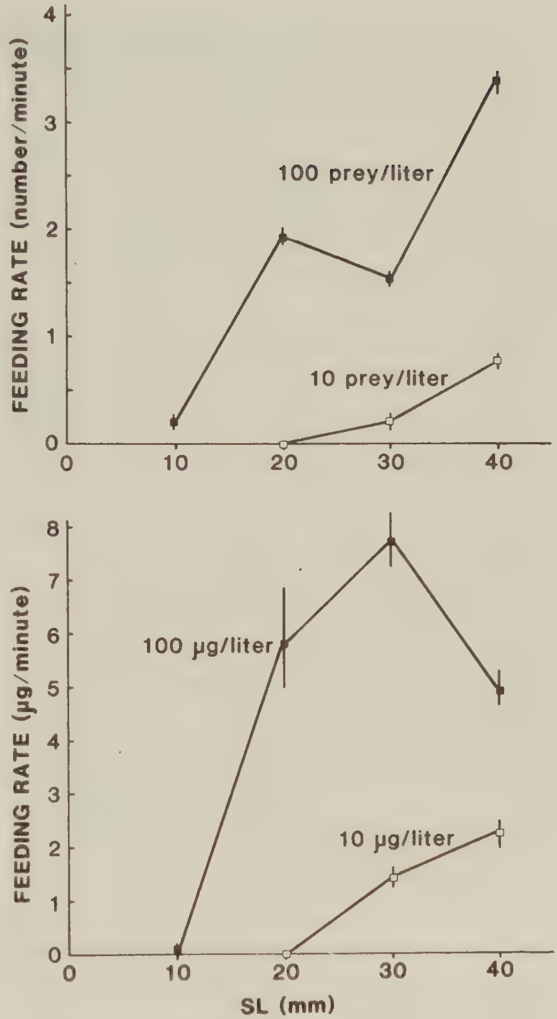

Figure 3. Estimated feeding rates of northern anchovy larvae of various sizes at two standardized prey concentrations. Rates are expressed as numbers of prey per minute and as weight of prey consumed per minute. The 95% confidence limits are indicated by vertical lines through each estimate.

According to the estimates, the 20- and 30-mm larvae would consume enough food to grow at observed rates at prey concentrations of 100/liter, but not at 10/liter. Thus, even late larvae (20-30 mm), which are able to select large prey, may require somewhat concentrated patches of food. On the other hand, 100 prey/liter is substantially lower than estimated food densities required for survival and growth in past studies (Hunter 1981), and is in keeping with the more recent

TABLE 3

Parameters for Multiple Linear Regression Equations* Describing Feeding Rate (ln rate + 1) in Relation to Larval Length (x_1) and Prey Concentration (x_2) for Northern Anchovy Larvae

SL (mm)	b_1	(Standard error)	b_2	(Standard error)	ln a	mult. r^2	F	p
Numbers of prey per minute								
10	−0.006	(0.012)	−0.7E-4	(0.5E-4)	0.243	0.107	1.97	0.16
20	0.025	(0.032)	0.013	(0.002)	−0.815	0.472	16.53	0.00
30	−0.015	(0.022)	0.008	(0.001)	0.491	0.556	23.18	0.00
40	−0.014	(0.017)	0.010	(0.001)	0.900	0.749	55.30	0.00
20-40	0.016	(0.005)	0.010	(0.001)	−0.463	0.666	116.64	0.00
Weight of prey per minute								
10	−0.002	(0.004)	−0.2E-4	(0.2E-4)	0.076	0.067	1.18	0.32
20	0.130	(0.041)	0.022	(0.004)	−3.032	0.557	23.25	0.00
30	0.052	(0.035)	0.014	(0.002)	−1.040	0.546	22.28	0.00
40	−0.037	(0.026)	0.007	(0.001)	2.282	0.664	36.62	0.00
20-40	0.002	(0.008)	0.008	(0.001)	0.556	0.528	65.31	0.00

*Model: $\ln(\text{rate} + 1) = \ln a + b_1x_1 + b_2x_2$

literature for larvae in general (Houde and Schekter 1980; Munk and Kiorboe 1985).

The prey concentrations used here were chosen to approximate high and low densities of prey suitable for *E. mordax* larvae in the field. Arthur (1977) states that the usual densities in areas where most anchovy larvae are found are about 1.5-4 copepodids/liter and about 13-30 nauplii/liter. The highest concentrations he reported from several studies in California Current waters were 36 copepodids/liter and 195 nauplii/liter. There are many difficulties in estimating field concentrations of appropriate-size prey on spatial scales relevant to larvae, especially because both prey sizes and foraging ranges change as larvae grow. Such estimates involve significant problems in sampling and data interpretation, since no single type of zooplankton gear adequately samples the entire size range of prey at one time and place, and different types of gear integrate densities over different scales—e.g., water bottles on a scale of decimeters (Owen 1981), pumps and nets over meters to kilometers (Beers and Stewart 1967; Arthur 1977). The prey distribution used in my experiments was skewed toward larger prey, with most experiments offering about 40% copepodids and adult copepods (range 30%-60%). This is about four times as many copepodids as larvae would normally encounter in the wild (Arthur 1977; Sheldon et al. 1977).

TABLE 4

Bioenergetic Estimates for *Engraulis mordax* Larvae Feeding at Two Prey Concentrations, Calculated for a 24-hr Period, with a 12-hr Feeding Period

SL (mm)	Dry weight (mg)	Metabolic requir. (μg)	Prey conc. (μg/l)	Consump. (μg)	Growth potential* (μg)	Growth body wt. (%)	Field growth (%)
10	0.316	1.808	100	43.2	28.4	9.0	15-20
			1,000	28.8	18.4	5.8	
20	4.185	10.941	10	0		—	—
			100	4,183.2	2,917.3	69.7	8-9
30	31.930	45.102	10	1,015.2	665.5	2.1	5-6
			100	5,400.0	3,734.9	11.7	
40	105.82	103.95	10	1,641.6	1,045.2	1.0	3-4
			100	3,715.2	2,496.7	2.4	

*calculated as consumption × assimilation efficiency − metabolic requirement.

In conclusion, these experiments indicate that feeding ability of northern anchovy larvae changes most dramatically between 10 and 20 mm SL. By 20 mm, the larvae's size selectivity is functionally similar to that of adults, in that larvae are capable of selecting the largest prey available over the range of sizes normally encountered. Koslow (1981) calculates that a spawning stock of $1.32\text{-}2.35 \times 10^6$ anchovies in the Southern California Bight would consume 10% to more than 100% of the secondary production available in the area. This implies that growth rates of late larvae may be limited by (1) intraspecific competition for large prey items with adults, (2) low prey concentrations, and (3) the stochastic interaction of these two factors.

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CARANGIDAE — Butaguchi

by Michael P. Seki

Valid name	*Pseudocaranx dentex* (Bloch and Schneider 1801) (Fig. 56)
Synonymy	(?) *Scomber adcensionis* Osbeck 1771 *Scomber cordila* (non-Linnaeus) Bonnaterre 1788 *Scomber dentex* Bloch and Schneider 1801 *Trachurus imperialis* Rafinesque 1810 *Caranx luna* Geoffroy Saint-Hillaire 1809 *Citula banksii* Risso 1826 *Caranx dentex* Cuvier 1833 *Caranx solea* Cuvier 1833 *Caranx analis* Cuvier 1833 *Selenia luna* Bonaparte 1846 *Caranx guara* Jordan and Evermann 1896 *Caranx cheilio* Snyder 1904 *Carangus cheilio* Jordan and Evermann 1905 *Uraspis cheilio* Jordan 1925 *Caranx ascensionis* (Osbeck) Fowler 1928 *Caranx adscensionis* (Osbeck) Smith 1949 (from Berry 1959; Fischer 1978)
Common and vernacular names	White trevally; thick-lipped trevally; butaguchi; buta ulua; pig ulua

Distribution

Uncommon in the main islands but abundant in the NWHI from the west bank of Nihoa to Kure Atoll. Inhabits not only banks and benthic slopes but also inshore areas. Found at depths between 18 and 183 m in the NMFS surveys. At Kure Atoll, HDAR field surveys found butaguchi in waters 1.5 m deep and occasionally in large schools of 200-300 individuals (Okamoto and Kawamoto 1980).

Distinguishing characteristics

D. VIII, I, 24-27; A. II, I, 20-23; P1. I, 19-20; Gr. 11-14+23-28 (Berry 1959; Fischer 1978). Body elongate, compressed; lips thick, fleshy, inferior jaw, unlike most of the other carangids; snout pointed, elongate in profile with a slight concave depression in the interorbital region.

In life, greenish blue dorsally becoming silver ventrally; a yellow stripe runs along the side of the body from the caudal peduncle through the eye. A distinctive black spot on posterodorsal edge of opercle; fins are yellow.

The NMFS samples from the NWHI ranged from 9.0 to 131.4 cm (0.05 to 11.5 kg).

Life history

Butaguchi in the NWHI are opportunistic bottom feeders (Seki 1984b). Of the stomach samples analyzed, fishes of the Families Congridae, Priacanthidae, and Serranidae, crustaceans such as crabs and shrimps, and octopuses were the most important. Time of feeding is unknown. Catch data suggest the species has a wide range of foraging grounds.

The functional length-weight relationship of 267 butaguchi (ranging from 33.3 to 89.0 cm) caught in the NWHI is:

$$W = 1.70 \times 10^{-8} L^{3.0074},$$

where W = weight (kg) and L = fork length (mm) (Uchiyama et al. 1984).

In NMFS age and growth studies, only a linear growth stanza was calculated because the largest fish examined had not reached the asymptotic growth phase. Preliminary estimates placed a 1-year-old at 30 cm and a 2-year-old at 66 cm.[10]

During the NMFS survey ripe ovaries were collected in January and July (Uchiyama and Tagami 1984).

Gear and catch

Butaguchi is taken principally by deep-sea handline, but has also been captured in traps.

Catch data are unavailable because the present statistical reporting system combines several species of carangids.

The species is scarce in the main islands; however, it is among the more abundant species in the NWHI and contributes significantly to the NWHI bottom fish landings (see footnote 6).

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[10] Uchiyama, J. H., J. Enitan, and J. D. Sampaga. Age and growth estimates of snappers and jacks of the Northwestern Hawaiian Islands. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396 (manuscr. in prep.).

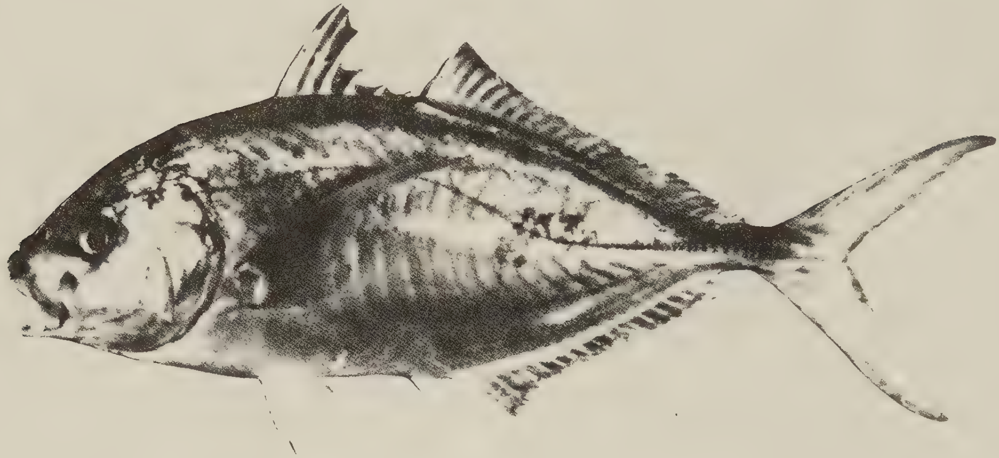

Figure 56.—*Pseudocaranx dentex*.

8691

CARANGIDAE ——— **Omilu**

by Michael P. Seki

Valid name	*Caranx melampygus* Cuvier and Valenciennes 1833 (Fig. 52)
Synonymy	*Caranx bixanthopterus* Rüppell 1835 *Caranx stellatus* Eydoux and Souleyet 1841 *Caranx medusicola* Jordan and Starks 1895 (from Berry 1965)
Common and vernacular names	Bluefin trevally; blue crevally; omilu

Distribution

Found throughout the Hawaiian Archipelago, captured from Necker Island to Pearl and Hermes Reef in the NWHI at depths from 2 to 183 m.

The adults of this species roam the inner and outer coral or rocky reefs singly or in small groups. The juveniles generally school in the shallow reef areas.

Distinguishing characteristics

D. VIII, I, 20-24 (usually 18-20); A. II, I, 17-20 (usually 18-19). Caudal forked and pectorals falcate (Williams 1958; Fischer and Whitehead 1974; Berry et al. 1981).

Two detached spines on the anal fin and scutes on the straight portion of the lateral line.

In life is usually greenish blue dorsally becoming silvery ventrally with many small blue-black spots covering the body, primarily on upper sides. The species may vary in color; sometimes a uniform bluish black with infrequent spotting.

Specimens from the NMFS surveys in the NWHI ranged from 9.3 to 71.0 cm FL.

Life history

The species is predominantly piscivorous (Randall 1980). Omilu feed most frequently in the early morning and late afternoon to evening mainly on fish and crustaceans (Hobson 1974). In the NWHI, omilu is primarily a diurnal piscivore (Okamoto and Kawamoto 1980).

No reproductive studies have been conducted on the omilu. Off East Africa, however, *C. melampygus* reached maturity at 30-40 cm (Williams 1965).

A length-weight relationship of 24 omilu ranging from 9.3 to 71.0 cm FL was:

$$W = 2.42 \times 10^{-5} L^{2.9412},$$

where W = weight (kg) and L = fork length (mm).

Gear and catch

Omilu is taken primarily by handline and traps. In 1961-79, the annual landings fluctuated between 410 and 4,292 kg, averaging 1,400 kg in the main islands. Omilu is considered as an incidental species among bottom fishing boats operating in the NWHI.

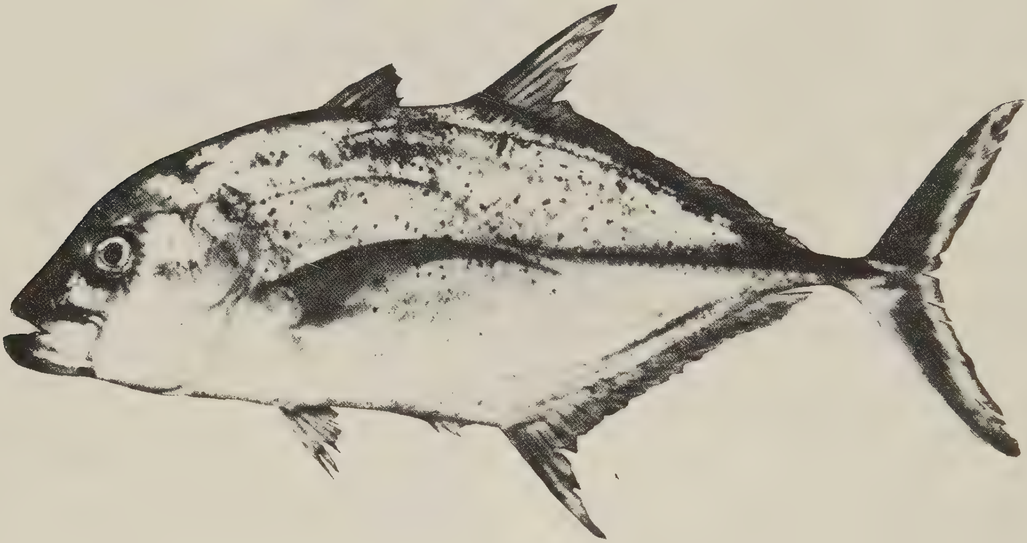

Figure 52.—*Caranx melampygus*.

by Michael P. Seki

Valid name	*Elagatis bipinnulata* (Quoy and Gaimard 1824) (Fig. 55)
Synonymy	*Seriola bipinnulata* Quoy and Gaimard 1824 *Elagatis bipinnulatus* Bennett 1840 *Seriolichthys bipinnulatus* Bleeker 1854 *Seriolichthys lineolatus* Day 1867 (from Weber and De Beaufort 1931)
Common and vernacular names	Rainbow runner; Hawaiian salmon; kamanu

Distribution

Circumtropical in warm temperate seas of the world (IGFA 1981). Distributed throughout the Hawaiian Archipelago.

Adult fish solitary, inhabiting surface waters of the open sea. Young have been known to frequent flotsam and may occur in small schools (Johnson 1978; IGFA 1981).

Distinguishing characteristics

D. VI, I, 25-30; A. I, I, 18-22 (the two detached terminal two-rayed finlets are included in the counts for both the dorsal and anal fins); Gr. 9-12+25-29. Lack scutes along the lateral line. Body slender, elongate, covered with ctenoid scales. Head and snout pointed, mouth small. Pectoral and pelvic fins short, about the same length; caudal fin forked (Fischer 1978; Johnson 1978).

In life, greenish blue dorsally becoming whitish silver ventrally, tinged with yellow. Two distinct blue bands, with a yellow band between them, run the length of the sides of the fish. The upper blue band begins just behind the eye, the lower at the snout, and both extend to the caudal peduncle. Fins greenish yellow.

The largest recorded specimen is 15.2 kg (IGFA 1981). Specimens taken in the NWHI ranged in size from 42.5 to 97.2 cm FL (2.5 to 10.2 kg).

Life history

In the tropical and subtropical Indo-Pacific, rainbow runner spawns throughout the year with a seasonal peak in March (Okiyama 1970). The larvae are the most abundant of the epipelagic carangids. Together with juveniles, the larvae are frequently associated with the pelagic sargassum community (Aprieto 1974).

Adults feed on crustaceans and fish (Fischer 1978). Copepods (mostly calanoid and *Corycaeus*) are the most important items in the diet of postlarvae and juveniles (Okiyama 1970).

A length-weight relationship of fish from Hawaiian waters is not available. For specimens from Guam and the Commonwealth of the Northern Marianas ranging from 40.2 to 89.1 cm FL, the relationship was:

$$W = 2.32 \times 10^{-4} L^{2.24},$$

where W = weight (kg) and L = fork length (mm).

Gear and catch

Rainbow runner is taken by trolling and occasionally by live bait, pole-and-line boats. Although it is an excellent food fish, the species does not contribute significantly to the commercial landings in Hawaii. In 1975-79, annual landings varied from 808 to 1,655 kg, averaging 1,196 kg.

There is no fishery for this species in the NWHI.

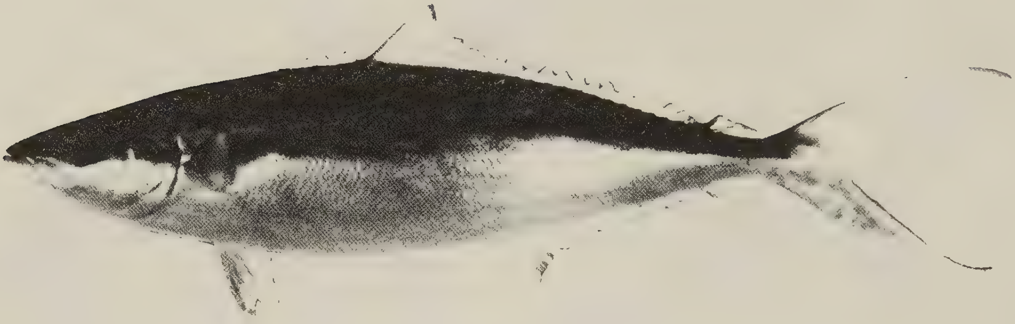

Figure 55.—*Elagatis bipinnulata.*

8693

CARANGIDAE — Ulua

by Michael P. Seki

Valid name	*Caranx ignobilis* (Forsskål 1775) (Fig. 51)
Synonymy	*Scomber ignobilis* Forsskål 1775 *Caranx hippoides* Jenkins 1903 *Caranx rhabdotus* Jenkins 1903 (from Gosline and Brock 1960)
Common and vernacular names	Giant trevally; jack; ulua (adult); papio (young); pauu; hon-ulua; sometimes called white ulua, a misnomer

Distribution

Widespread in the main islands. Captured anywhere from the shoreline through the reef flats to the benthic slopes in waters from the surface to depths of 91 m at almost all islands and banks from Necker Island to Kure Atoll.

Distinguishing characteristics

D. VIII-I, 18-21 (usually 19-20); A. II-I, 15-17 (usually 16); P1. I, 18-20. Body deep, slightly compressed, with a steep, strongly curved head, snout blunt. Breast mostly naked, a small central patch of scales may be covered with skin just anterior to pelvic fins. Scutes or plates along the straight portion of the lateral line scales 28-30 (Williams 1958; Fischer and Whitehead 1974; Berry et al. 1981).

Varies from silvery to black in life. Large fish may have small black spots on upper sides of the body. Color differences in ulua are associated with sex and maturity (Talbot and Williams 1956). Mature males possess dusky to black bodies, heads, and fins; whereas mature females have bodies and heads that are pale to silvery.

Ulua is the largest species of the genus; maximum verified size is 146.0 cm FL, and 52.6 kg (Berry et al. 1981). Specimens from 20.7 to 133.0 cm FL (mean 74.4 cm) were collected in the NWHI.

Life history

Observations of natural spawning of *Caranx ignobilis* in the Philippines showed two spawning seasons, one in December-January and the other in June. Spawning occurred during the day, close to shore (Von Westernhagen 1974). Size at maturity was estimated to be 54-61 cm FL (Williams 1965). There is also a possibility that segregation by sexes occurs immediately before spawning takes place.

Feeding studies in the NWHI revealed that the species is primarily a nocturnal piscivore, although cephalopods and crustaceans were also significant in the diet (Okamoto and Kawamoto 1980; Parrish et al. 1980). Similar diet and feeding behavior were found for the species off East Africa (Williams 1965). Of particular interest is that ulua may also prey voraciously on sublegal and berried lobsters which have been released at the surface from commercial fishing vessels (Gooding 1985[9]).

A length-weight relationship of 124 ulua, ranging from 20.7 to 133.0 cm FL caught in the NWHI was:

$$W = 2.73 \times 10^{-5} L^{2.9131},$$

where W = weight (kg) and L = fork length (mm).

Gear and catch

Taken primarily by handline and traps; it is also one of the target species in recreational fishing and may be caught with bottom set line or by casting from shore with rod and reel.

Ulua is one of the dominant species of the jack fishery in Hawaii. The statewide annual landings of ulua (including several species of carangids) in 1961-79 varied between 19,647 and 55,494 kg and averaged 35,692 kg.

Highly esteemed by the local population, the ulua is one of the target species of bottom fishing boats operating in the NWHI.

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[9] Gooding, R. M. 1982. Predation on surface and bottom released spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, Admin. Rep. H-82-1, 20 p

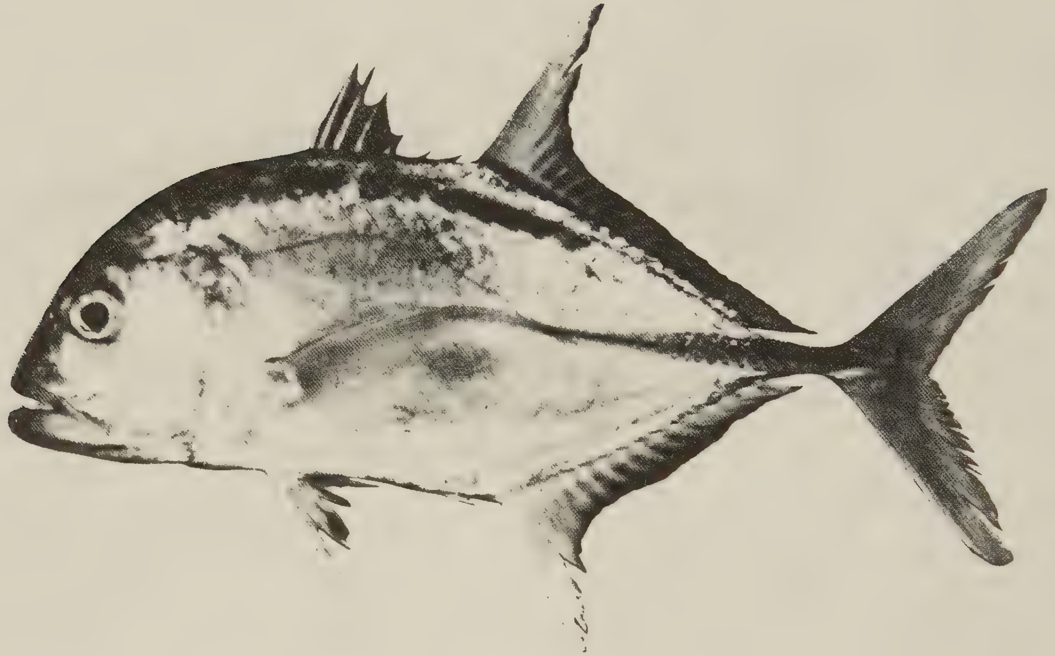

Figure 51.—*Caranx ignoblis.*

by Michael P. Seki

Valid name	*Epinephelus quernus* Seale 1901 (Fig. 49)
Synonymy	None
Common and vernacular names	Seale's grouper; grouper; sea bass; hapuupuu

Distribution

Known only from Hawaiian waters (Tinker 1978). Present at all islands and banks from Middle Bank to Bank No. 11 at depths from 18 to 230 m. Large numbers observed in waters as shallow as 5 m at Kure Atoll and Midway (Hobson 1980). No pattern of spatial distribution by age and size shown (Ralston 1980).

Distinguishing characteristics

D. XI, 14-15; A. III, 9; Pc. 19; P1. I,5; Gr. 7+16 (Seale 1901; Jordan and Evermann 1905). Body oblong, girth greatest posterior of nape becoming laterally compressed caudad; covered with small ctenoid scales; posterior edges of dorsal and anal soft rays and caudal fin rounded.

Like other groupers, this species has a large protractile mouth with maxillary reaching posterior of the orbit. Preoperculum is finely serrated along upper edge.

In life, varies from purplish brown to nearly black, they may be covered, particularly along the sides, with small light blue or white spots. Differences in body color between individuals may be attributable to physiological stress, behavioral responses, or the environment.

Life history

Little is known about this species. The spawning period of hapuupuu has not been determined throughout the Hawaiian chain; however, ovaries with hydrated eggs have been collected from January through early April in the NWHI indicating winter spawning in that area (Uchiyama and Tagami 1984; Kikkawa[8]). Other aspects of reproduction such as fecundity, number of spawnings per season, and hermaphroditism remain to be examined.

Hapuupuu are carnivorous, opportunistic bottom feeders (Seki 1984a). Among spew samples analyzed, pandalid shrimps, lutjanids, emmelichthids, and conger eels were most important. Cephalopods (mainly octopods) and crabs also occurred among the forage items.

A functional length-weight relationship of 547 hapuupuu ranging from 23.8 to 110.6 cm is:

$$W = 9.29 \times 10^{-9} L^{3.1028},$$

where W = weight (kg) and L = total length (mm) (Uchiyama et al. 1984).

Gear and catch

This species is usually taken with handline although it is also caught incidentally in traps and pots. Hapuupuu is the only serranid contributing significantly to the commercial landings in Hawaii. During 1961-79, the annual landings ranged from 9,311 to 33,799 kg, averaging 17,725 kg. The species ranked 21st among commercial marine species landed during this period.

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[8] Kikkawa, B. S., Research Assistant, Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, pers. commun. May 1982.

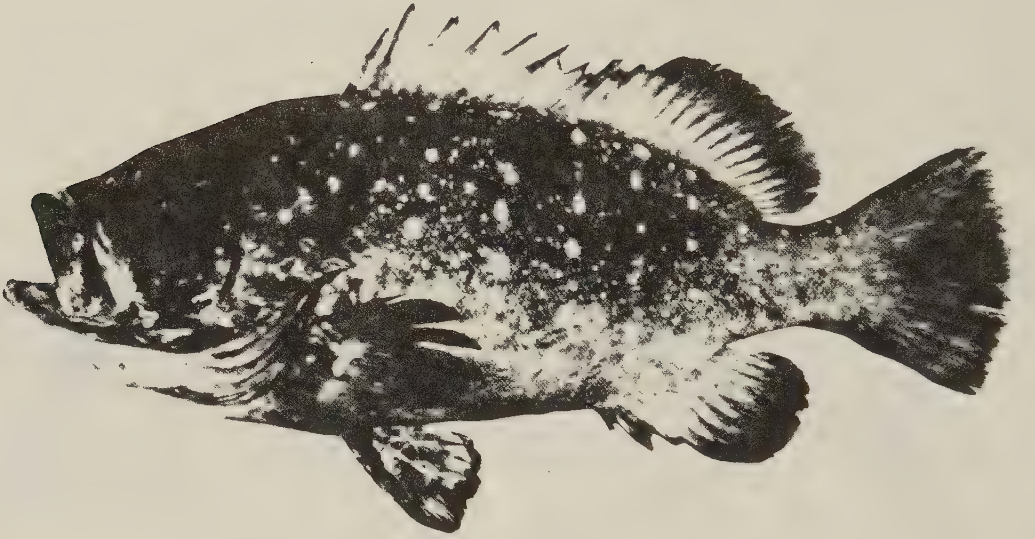


Figure 49.—*Epinephelus quernus*.

8695

Review and Present Status of Handline and Bottom Longline Fisheries for Alfonsin

MICHAEL P. SEKI
DARRYL T. TAGAMI
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96822-2396

ABSTRACT

The pelagic armorhead, *Pseudopentaceros wheeleri*, and the alfonsin, *Beryx splendens*, are the principal target species in the central North Pacific seamount groundfish fishery. The present fishery, executed predominantly by the Japanese, uses bottom trawls to harvest the resource, although in the past a hook-and-line fishery was also active at the seamounts primarily targeting the more valuable alfonsin.

The beginning of the Japanese hook-and-line fishery for alfonsin dates back to 1875, when vessels restricted operations to nearby fishing grounds off Chiba Prefecture and Shimoda. The fishery has since grown and now includes vessels over 100 tons which operate in waters near the Nansei Islands and the Zunan area. The fishing ground around Midway, which was also fished by hook-and-line boats, has been abandoned in recent years.

Since 1976, the Southwest Fisheries Center Honolulu Laboratory has conducted limited exploratory resource surveys at the seamounts of the southern Emperor-northern Hawaiian Ridge, with emphasis at Hancock Seamounts. Vertical handlines were used to assess the resources of the seamount slopes and other untrawlable areas. Pelagic armorhead dominated the handline catch, and alfonsin, dogfish, *Squalus* sp., and medai, *Hyperoglyphe japonica*, were the most abundant of the other species taken. The surveys indicated that the alfonsin caught on the slopes with handlines were larger than those taken on the summit by trawling. For pelagic armorhead, the sizes of handline- and trawl-caught fish were similar.

Test marketing of four species of frozen seamount groundfishes through the Honolulu fish auction and retail outlets indicated that product promotion would be necessary to develop a commercially feasible domestic fishery for the various species.

INTRODUCTION

The central North Pacific seamount groundfish fishery exploits a complex of species, principally the pelagic armorhead or kusakari tsubodai, *Pseudopentaceros wheeleri*, and the alfonsin or kinmedai, *Beryx splendens*. Since 1969, the major effort expended at the seamounts by the Japanese and the Soviets to exploit the resource has involved trawling. Although alfonsin represents the second species of importance in the seamount trawl fishery, it constitutes only a small percentage of the catch and is considered an incidental species (Humphreys et al. 1984). Furthermore, due to the rough and steep topography of the summits and slopes, many of the seamount areas inhabited by alfonsin are untrawlable even with modern techniques and gear. Vertical handlines and bottom longlines can fish in areas inaccessible to trawlers and have thus been the main fishing methods for alfonsin (Masuzawa et al. 1975; Sasaki 1978). This report reviews the available information, and presents the status of current research activity, on the hook-and-line fisheries for alfonsin.

TARGET SPECIES

Fishes of the genus *Beryx* (Fig. 1) are valued as food in Tokyo and neighboring prefectures. The most common and valued of the *Beryx* species is the alfonsin, *B. splendens*. This bright red fish which inhabits rocky bottom several hundred meters deep is the primary target species in the seamount bottom longline and handline fisheries (Abe 1969; Uchida and Tagami 1984). The Pacific distribution of this species includes the central North Pacific seamounts (from Koko Seamount to Seamount 11 within the southern Emperor-northern Hawaiian Ridge (SE-NHR)) and in the South Pacific along the Lau (South Fiji) Ridge (Sasaki 1978; Humphreys et al. 1984). In the western Pacific where the largest alfonsin fishery exists, its distribution includes Sagami Bay and Kashima Nada, the Izu Islands, the Kinan Seamounts, and the Kyushu-Palau Ridge (Chikuni 1971; Sasaki 1978). The optimum temperature range for alfonsin is reported to be 6° to 18°C (Onishi and Sato 1970).

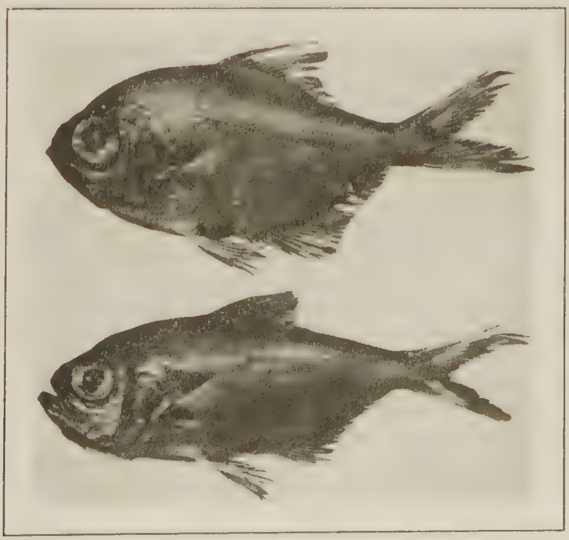


Figure 1.—Specimens of alfonsin, genus *Beryx*. Upper specimen is *B. decadactylus* and the lower specimen, *B. splendens*.

The broad alfonsin or nanyokinme, *B. decadactylus*, is also bright red and appears to inhabit areas similar to those inhabited by *B. splendens*. This species has often been taken with *B. splendens* but in much smaller numbers. *Beryx decadactylus* can be distinguished from *B. splendens* by its deeper body, larger, rougher scales, and prominent preorbital spine (Uchida and Uchiyama 1986). The Pacific distribution of this species also includes the seamounts within the SE-NHR; however, unlike *B. splendens*, *B. decadactylus* can also be found farther south throughout the Hawaiian Archipelago. In Japanese waters, the broad alfonsin has been captured from Sagami and Suruga Bays, the Sea of Japan from Wonsan to Pusan, and the Kyushu-Palau Ridge. In the South Pacific, the broad alfonsin is known from the Campbell (New Zealand) Plateau (Busakhin 1982; Okamura et al. 1982).

A third congener, *B. mollis*, was captured by hook-and-line fishermen in Sagami Bay. Known in Japan as fusenkinme, it is considered a rare species. At present, the distribution of *B. mollis* is apparently limited to the waters of Sagami Bay (Abe 1959; Busakhin 1982).

In addition to the alfonsin, other less valuable species caught in the bottom longline and handline fishery are *Hyperoglyphe japonica* (medai), *Paracaesio caeruleus* (aodai), *Erilepis zonifer* (aburaboozu), *Helicolenus hilgendorfi* (yumekasago), *Sebastes* sp. (akodai), and *Epinephelus* sp. (kue) (Masuzawa et al. 1975; Suisan Sekai 1976; Sasaki 1978).

THE FISHERY

The hook-and-line fishery for alfonsin, primarily in the area from Sagami Bay to the Izu Islands, has existed in Japan for many years. Although the history of the fishery is not well-known, it appears that around 1875, vessels from Misaki fished for alfonsin, medai, and mutsu, *Scombrops boops*, off Chiba Prefecture and Shimoda. Around 1915-16, the fishery expanded to the Izu Islands area as more of the vessels became powered by engines. By the 1970's, over 1,400 boats were participating to some degree in the groundfish fishery, although not all the vessels targeted alfonsin (Masuzawa et al. 1975). Annual landings of alfonsin alone exceeded 1,000 metric tons (MT) in Tokyo and neighboring prefectures (Abe 1969).

The size of vessels in the Japanese fishery varies from under 5 tons to over 100 tons. The small vessels fish mainly just offshore from their home ports whereas the large vessels fish near the Nansei Islands and the Zunan area. Some of the large, 20- to 100-ton vessels have operated in the Midway area of the SE-NHR, usually targeting alfonsin (Masuzawa et al. 1975).

Although the alfonsin resource on the central North Pacific seamounts had been discovered by Soviet trawlers in 1967 (Sakiura 1972), it was not until around 1973 that the Japanese initiated fishing for alfonsin with hook and line at Milwaukee Seamounts (Masuzawa et al. 1975). Since that time, vessels from Korea and Taiwan have joined the fishery (Suisan Sekai 1976; [Hawaii.] Department of Land and Natural Resources 1979). In 1975, the Japanese hook-and-line fishery in the SE-NHR took about 4,000 MT of groundfish, of which about 500 MT were caught within the 200-mile U.S. Fishery Conservation Zone (FCZ) and also harvested about 500-600 MT of alfonsin and other groundfishes off Guam and the Northern Mariana Islands (Federal Register 1977). Little else, however, is known about the activity of vessels in this "open fishery" which does not require permits or licenses (Sasaki 1978).

In 1977, the National Oceanic and Atmospheric Administration (NOAA), Department of Commerce, put into effect a Preliminary Fishery Management Plan to regulate foreign fishing for groundfishes at the seamounts, specifically the Hancock Seamounts within the FCZ. Since then, foreign fishing for seamount groundfishes has been exclusively conducted by trawling, and hook-and-line operations for alfonsin around Midway have ceased.

UNITED STATES RESEARCH

From 1976 to 1981, the Southwest Fisheries Center (SWFC) Honolulu Laboratory, National Marine Fisheries Service (NMFS), participated in a cooperative investigation of the marine resources of the Northwestern Hawaiian Islands (NWHI) (Fig. 2). Within the scope of the NWHI studies, limited surveys of the fishery resources of the seamounts within the Hawaiian Archipelago, particularly at Hancock Seamounts, were conducted. The SWFC has since initiated a program to further survey the seamount resources of the SE-NHR, including Koko, Kammu, Colahan, Hancock, and Seamount 11.

Methods

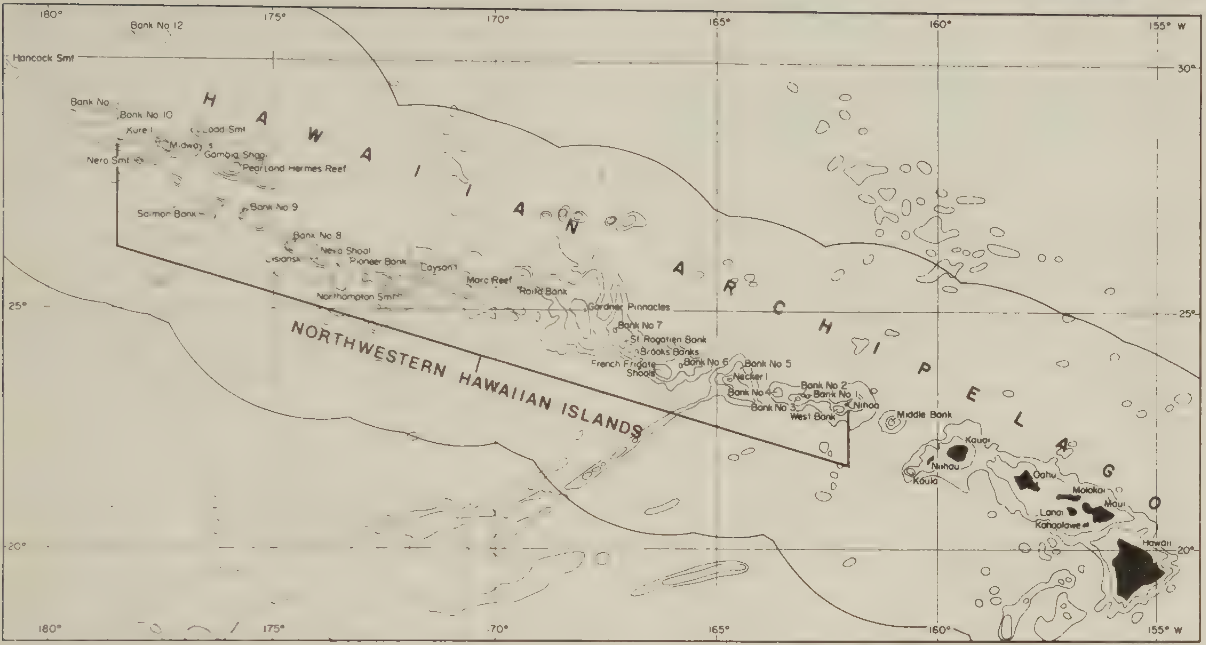
One of the principal fishing methods employed by the SWFC to assess the distribution and abundance of seamount species was the vertical handline which in general was similar to the Hawaiian deep-sea handline gear described by Uchida and Uchiyama (1986). Usually, hydraulic powered gurdies were employed to haul in the line, but in some early cruises hand retrieval or electric reels (gurdies) were used. The gurdies spooled approximately 1,100 m of 118-kg test, hard-braided nylon line attached to a terminal rig consisting of a drop line (about 1.5 m long, 113-kg test monofilament leader) separated by three-way swivels, hook lines (about 0.5 m long, 13.6-kg test monofilament leader), recurved "circle" hooks, and a 1.4- to 2.3-kg lead weight (Fig. 3). The size of hook varied depending on the target species. For alfonsin, we normally used No. 18 to 22 hooks, although some large fish were taken on No. 28 to 30 hooks. The number of hooks per line varied from 5 to 20 but was normally 10 to 12, each usually baited with stripped squid. Fishing was done day and night while the vessel drifted over banks 146-640 m (80-350 fathoms) deep.

Results and discussion

The major effort to sample groundfishes with handlines was concentrated at Southeast (SE) and Northwest (NW) Hancock Seamounts and Seamount 11. At SE and NW Hancock (total effort was 1,059.0 and 1,278.6 hook-h, respectively) pelagic armorhead dominated the catch, constituting 59.2% of the total fishes caught at SE Hancock and 75.4% taken at NW Hancock (Table 1). Alfonsin comprised 5.8 and 12.2% of the fishes taken at SE and NW Hancock, respectively. The greatest depth of capture was about 640 m for alfonsin and about 510 m for pelagic armorhead. Major incidental species of commercial value were *Hozukius guyotensis* and *Helicolenus avius*, which are fishes closely related to the akodai and the yumekasago, dogfish, *Squalus* sp., and medai.

At Seamount 11, 437.0 hook-h of handlining were conducted; dogfish (48.2%), alfonsin (21.1%), and pelagic armorhead (12.3%) comprised the majority of the catch. The grouper, *Epinephelus quernus*, was also taken here which reflects a transition of ichthyofauna from the armorhead-alfonsin complex characteristic of the SE-NHR seamounts to the tropical snapper-grouper complex that characterizes

8692


180°
175°
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Hancock Smt
Bank No 12
Bank No 11
Bank No 10
Kure I
Ladd Smt
Midway Is
Nero Smt
Gambia Shoal
Pearl and Hermes Reef
Salmon Bank
Bank No 9
Bank No 8
Lisianski
Nero Shoal
Pioneer Bank
Laysan I
Maro Reef
Raita Bank
Northampton Smt
Gardner Pinnacles
Bank No 7
St Rogatien Bank
Brooks Banks
French Frigate Shoals
Bank No 6
Bank No 5
Necker I
Bank No 4
Bank No 3
Bank No 2
Bank No 1
West Bank
Nihoa
Middle Bank
Kauai
Niihau
Kaula
Oahu
Molokai
Maui
Lanai
Kahoolawe
Hawaii
HAWAIIAN ARCHIPELAGO
NORTHWESTERN HAWAIIAN ISLANDS

Figure 2.—The Hawaiian Archipelago, including the Northwestern Hawaiian Islands.

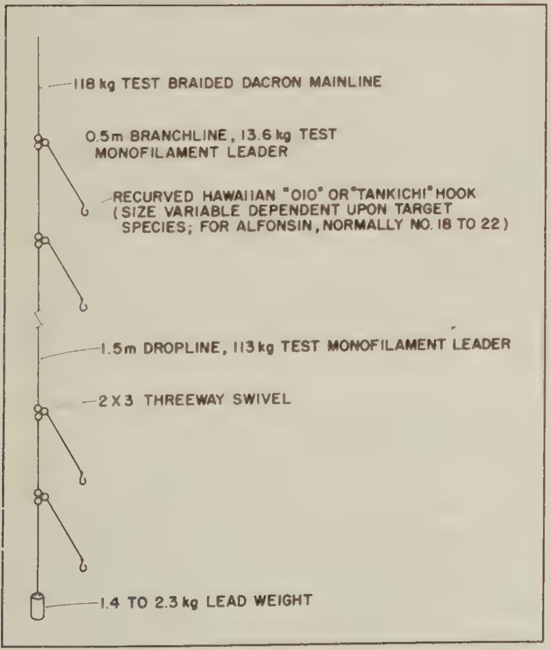
118 kg TEST BRAIDED DACRON MAINLINE
0.5 m BRANCHLINE, 13.6 kg TEST MONOFILAMENT LEADER
RECURVED HAWAIIAN "OIO" OR "TANKICHI" HOOK (SIZE VARIABLE DEPENDENT UPON TARGET SPECIES; FOR ALFONSIN, NORMALLY NO. 18 TO 22)
1.5 m DROPLINE, 113 kg TEST MONOFILAMENT LEADER
2 X 3 THREEWAY SWIVEL
1.4 TO 2.3 kg LEAD WEIGHT

Figure 3.—Terminal rig of Hawaiian deep-sea handline gear when fishing for alfonsin, *Beryx splendens*.

Table 1.—Total number and catch per unit effort (CPUE × 10^{-1}) (by hook-h) of groundfish taken by handline at three seamounts along the northern Hawaiian Ridge.

	SE Hancock		NW Hancock		Seamount 11	
	No.	CPUE	No.	CPUE	No.	CPUE
Etmopterus sp.	2	0.02	1	0.01	1	0.02
Squalus sp.	51	0.48	11	0.09	55	1.26
Polymixia berndti	9	0.08	4	0.03		
Moridae	1	0.01	1	0.01		
Macrouridae					1	0.02
Beryx splendens	24	0.23	55	0.43	24	0.55
Hozukius guyotensis	11	0.10	10	0.08		
Helicolenus avius	2	0.02				
Scorpaenidae					1	0.02
Epinephelus quernus					4	0.09
Plectranthias kelloggi	2	0.02	2	0.02		
Cookeola boops					6	0.14
Decapterus tabl	12	0.11	5	0.04		
Pseudopentaceros wheeleri	247	2.33	341	2.67	14	0.32
Parapercis sp.	1	0.01				
Scomber japonicus	44	0.42	2	0.02		
Promethichthys prometheus	1	0.01			8	0.18
Ruvettus pretiosus	1	0.01				
Hyperoglyphe japonica	9	0.08	20	0.16		
Total fishes	417	3.94	452	3.53	114	2.61

the NWHI banks south of Kure Atoll. Humphreys et al. (1984) attributed the sharp demarcation of the ichthyofauna around the 180th meridian to differences in summit depth and temperature.

Little effort was expended at other seamounts in the SE-NHR. At Koko Seamount, 73.2 hook-h of fishing produced 11 *H. avius*, and at Kammu Seamount, 6 pelagic armorhead and 4 dogfish were taken in 140.0 hook-h. Twenty pelagic armorhead, 1 dogfish, 1 medai, and 1 broad alfonsin were caught at Colahan Seamount in 80.4 hook-h of fishing and at Yuryaku Seamount, there was no catch in 36.0 hook-h.

The SWFC surveys have shown that alfonsin caught on the slopes with handlines were significantly larger than those taken on the summit by trawling ($F = 4{,}644.6$; $df = 1{,}562$; $P < 0.0001$). Handline-caught alfonsin from the slope ranged from 24.3 to 41.3 cm standard length (SL) and averaged 33.0 cm SL but trawl-caught alfonsin from the summit ranged from 12.5 to 31.5 cm SL and averaged only 16.5 cm SL (Fig. 4). Since most of the trawl-caught alfonsin from the summit were juveniles and those caught on the slope were adults, this difference in size classes between the two habitats may be attributed to depth preference of the age classes. Our results corroborate the findings by Iguchi (1973) who reported that alfonsin taken from seamounts in the SE-NHR at depths >400 m averaged 37.7-38.4 cm, whereas those taken in depths <300 m were composed of two modal size classes at 16.8 and 21.9 cm. He postulated that alfonsin initially occupy relatively shallow waters as juveniles and progressively move into deeper water as they grow larger.

The size of handline- and trawl-caught pelagic armorhead was similar, although large specimens of *P. wheeleri* (49.5-54.7 cm total length, 2.0-3.4 kg) have been hooked in deep waters at French Frigate Shoals, Ladd Seamount, and Kure Atoll in the NWHI (Randall 1980; Tagami and Humphreys in prep). The occurrence of this species as far south as French Frigate Shoals has spurred speculation that the distributional range of pelagic armorhead through the Hawaiian Archipelago is much wider than previously believed.

To test consumer reaction, approximately 240 kg of four species of frozen groundfishes from the seamounts were placed on sale in July 1983 through the Honolulu fish auction. The akodai-like *H. guyotensis* received the highest prices ranging from $0.25 to $0.57/kg. Alfonsin also received $0.25/kg, whereas pelagic armorhead received $0.23/kg and medai received $0.11/kg. The pelagic armorhead were taken by trawl and handline, whereas the other three species were captured exclusively with hook and line. The limited market test suggested that product promotion would be necessary to develop a commercially feasible domestic fishery for seamount species. Similarly when pelagic armorhead was initially marketed in Japan, it met stiff consumer resistance. Extensive advertising and sales promotion there, however, boosted market demands ([U.S.] NMFS 1975).

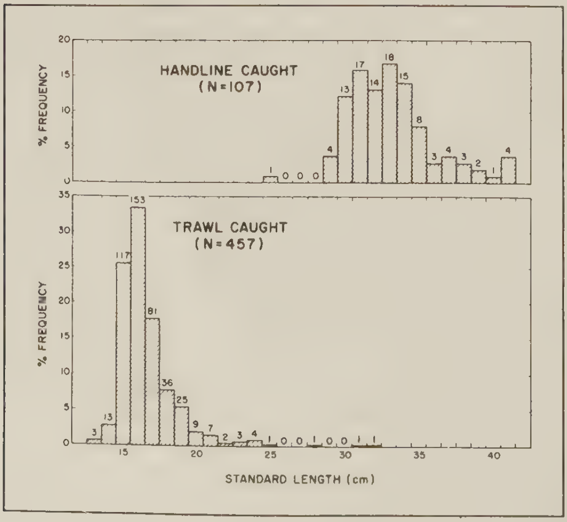

Figure 4.—Length-frequency comparison of handline versus trawl-caught alfonsin, *Beryx splendens*.

OTHER RESEARCH

Exploratory surveys for deep groundfish were initiated by the Pacific Tuna Development Foundation (PTDF) through the Government of Guam in 1980 and the State of Hawaii in 1981. In both surveys, the chartered fishing vessels used primarily vertical handlines, similar to the gear described earlier.

The PTDF-Guam surveys, conducted on the deep banks and seamounts of the South Honshu Ridge and around the Northern Mariana Islands, targeted depths from 40 to 640 m (22-350 fathoms); most of the effort was focused at depths <274 m (150 fathoms). As a result, the catch was composed primarily of fishes in the tropical snapper-grouper complex. Limited effort in waters deeper than 366 m (200 fathoms) yielded occasional catches of polymixiids, gempylids, and squalids (Hosmer and Kami 1981). Although the alfonsin was targeted during the surveys, none was taken. In 1977, however, two chartered Korean vessels with bottom longline gear caught 15 broad alfonsin in the Northern Marianas. Another Japanese vessel under charter to the Commonwealth of the Northern Mariana Islands caught about 227 kg (500 lb) of broad alfonsin near Saipan with a bottom gill net (Uchida 1983).

The broad alfonsin, the pomfret, *Eumegistus illustrus*, and other groundfishes that inhabit depths greater than those usual for commercially valuable snappers and groupers were sought during exploratory surveys conducted around the main Hawaiian Islands by the PTDF and the Hawaii State Department of Land and Natural Resources. Only a single broad alfonsin off Lanai and two off Oahu in depths of about 320 m (175 fathoms) were taken; however, the pomfret was moderately abundant (75 caught, 72.2% of the catch by weight) and appeared to hold the most potential as a new deep groundfish resource. In a consumer acceptance test at the Honolulu fish auction, fresh pomfret received prices ranging from $0.39 to $0.82/kg while fresh broad alfonsin received $0.45/kg (Okamoto 1982).

FUTURE RESEARCH AND CONCLUSIONS

A major problem of deep-sea multihook gear has been the tangling of hooks. A proposed solution involves the use of terminal rigs with dropper lines constructed of polyvinyl chloride pipes, which can be utilized on vertical handlines as well as on bottom longlines. This experimental gear, originally devised in the eastern Caribbean Sea for use over extremely rocky bottom and to alleviate the hauling effort, was found to be extremely successful and effectively caught all the species of snapper inhabiting waters down to 549 m (300 fathoms) (Crowley 1982). In depths of 183-366 m (100-200 fathoms), 3,000 or more hooks could be set and hauled by a three-man crew in one day compared with no more than 1,500 hooks set and hauled in a day with conventional nylon gear.

In conclusion, preliminary findings reveal the existence of a potentially exploitable groundfish resource in the SE-NHR seamounts; however, we need to determine the feasibility of a domestic hook-and-line fishery on these slopes and to decide how such a resource should be managed. The feasiblity of such a domestic fishery will ultimately depend on whether market prices will cover the inevitably high operational costs.

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8696

METHODOLOGICAL PROBLEMS IN SAMPLING COMMERCIAL ROCKFISH LANDINGS

A. R. Sen[1]

ABSTRACT

The present sample survey plan, for the estimation of age and species composition of California rockfish landings, which is stratified two-stage with port-month group as a stratum, poses serious operational problems in data collection. A revised plan is suggested which is workable. Formulas have been developed for estimating total catch and its error by species-sex-age groups; optimum sampling and subsampling fractions have been obtained for a given cost function and the precision of the estimator is compared with two other estimators. The method developed has been extended to cover situations other than rockfish.

The paper also deals with double-sampling for specified cost for the estimation of age composition of a species, which is important to predict the status of a stock in future years, the inherent problems in data collection in commercial fisheries, and the measurement errors involved in the survey.

Estimates of the total catch (in terms of number) by species-sex-age and by area of landing and during a given time for commercial rockfish caught in California north of point Arguello are currently based on a probability sample of landings. The commercially important species of rockfish taken by California's fishery with mixed species are widow rockfish, *Sebastes entomelas*; bocaccio, *Sebastes paucispinis*; and chilipepper, *Sebastes goodei*.

A study was undertaken during 1983 under agreement between the present author, the Humboldt State University Foundation, and the Tiburon Laboratory of the National Marine Fisheries Service, NOAA, to determine if the present sampling plan for the estimation of species and age-composition of California rockfish landings is workable. The study revealed that the current plan is not operationally feasible. A revised plan is proposed which is workable and would provide efficient estimates of the parameters based on existing catch data within the usual limitations of budget and personnel and under the assumptions made in the plan. Formulas have been developed for the ratio estimators of mean and total catch and their errors. Optimum sampling and subsampling fractions have been obtained for a given cost function and the precision of the estimator is compared with two other estimators.

For most theoretical population work and for management purposes, the knowledge of the age composition is important to predict the status of the stock in future years. Fridricksson (1934) developed the age-length key method for determing age composition from a large number of length measurements. Fridricksson's approach was improved by Ketchen (1950) who provided more accurate results for age groups at the extremities of the distribution. Kutkuhn (1963) mentioned the limitations of the age-length key approach except in situations where price differentials may demand sorting of landings by size criterion. Westrheim and Ricker (1978) pointed out that the age-length key approach will almost always give biased estimates. Clark (1981) and more recently Bartoo and Parker (1983) dealt with methods for control or elimination of bias. Following the method of Tanaka (1953) in which stratification occurs after subsampling for age, Kutkuhn (1963) estimated absolute age composition of California salmon landings by port-month groups. He showed that the sampling procedure is not effective unless the age sample is at least five times costlier than the length sample.

Mackett (1963) found double sampling more efficient than simple random sampling with fixed sampling costs for estimating relative age composition of Pacific albacore landings.

Southward (1976) found that a sample of otoliths proportional to the length frequency of sampled fish from each port was preferable to fixed sample size procedure for estimating age composition of Pacific halibut. Kimura (1977) arrived at the same conclusion as Southward by following a somewhat different approach.

We will present some of the important considera-

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[1] Department of Mathematics and Statistics, Queen's University, Kingston, Ontario, Canada K7L 3N6; present address: 67 Ranch-Ridge Way N.W., Calgary, Alberta, Canada T3G 1Z8.

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tions in sampling for estimating age composition of rockfish landings based on recent widow rockfish data from the California coast. Finally, we will describe some of the measurement errors, which would normally occur in simple random sample of individual fish and which are taken care of in cluster sampling adopted in our approach.

The sampling plan arrived at may produce usable results under the assumptions stated, though some of the assumptions have been under attack during recent years.

DESIGN OF THE SURVEY

Rockfish are being landed at 14 points on the California coast. Of these, three cater only to commercial fishing, four to sport fishing, and seven to both sport and commercial fishing. The 10 commercial ports are grouped into 6 port groups with a sampler (six in all) assigned to each of the 6 ports—Eureka, Fort Bragg, Bodega Bay, San Francisco, Monterey, and Morro Bay.

The commercial trawlers make trips varying in length from 1 to 8 d. These vessels maintain log books to keep records of area fished and appropriate catch for each tow. Sampling by tow is generally not feasible because it is not possible for the sampler to be on board during haul time. For the same reasons no estimates of fish being rejected and returned to the sea are obtained because this would involve collection of discarded fish from randomly selected tows within sampled trips.

Selection Procedure

A two-stage stratified random sampling plan was adopted with port-month group as a stratum and boat trips within a stratum as first-stage sampling units. Fish are sorted at sea into market categories. The first stage sampling units are poststratified into categories and at least one cluster of a given weight is subsampled within each sort-type from a first-stage sampling unit. Categories are based upon species composition, size, and quality, but in other contexts they could be strictly size or species categories. Cluster (box) of 25 lb is taken when sampling small fish, or any time small rockfish are landed such that there would be more than 20 fish in the 50-lb cluster. In all other cases 50-lb standard cluster size is selected. A cluster is next separated by number of each species and its weight, which are recorded along with sex, total length, and otolith of each member of a species in the cluster.

The instructions are to "sample all market categories (sorts) from a boat, and from as many boats as possible and select:

"(i) 1 cluster per 20,000 lb of widow rockfish landed by each boat, up to 4 clusters,
"(ii) 1 cluster for all other species, if less than 5,000 lb landed, and
"(iii) 2 clusters for all species if more than 5,000 lb are landed.

"The second cluster should not be taken if this precludes sampling another boat."

Estimation with Poststratification of Sample Trips by Categories

Consider the problem of estimation of total catch of a given species for a port-month stratum. Equations for estimation of other characteristics for fisheries with mixed species are straightforward and can be obtained by substituting the value of the characteristic for the catch of the species. Totals across strata are formed by simple additon.

Notation

For a given species, let

N = total number of trips,
n = number of randomly sampled trips,
W = total weight of fish caught from all trips,
W_i = weight of fish caught on trip i,
W_{ij} = weight of fish for sort j caught in trip i,
m_{ij} = number of clusters sampled from sort j on trip i,
m_i = number of clusters sampled on trip i,
m = number of clusters sampled over n trips,
$W_i = \sum_j^{L_i} W_{ij}$ where L_i is the number of sorts in trip i,
y_{ijk} = number of fish of the species in cluster k from sort j of trip i,
Y_{ij} = total number of the species caught from sort j of trip i,
Y = total number of species caught from all trips,
$\bar{\bar{Y}}$ = mean catch per cluster for the species,
$\bar{y}_{ij} = \sum_k y_{ijk}/m_{ij}$ = unbiased estimate of $\bar{Y}_{ij}$,
w_{ijk} = weight of the kth cluster from the jth sort of the ith trip,
$\hat{M}_i = \dfrac{W_i}{\bar{w}_i}$ where $\bar{w}_i = \sum_j \sum_k w_{ijk} / \sum_j m_{ij} =$

average weight of sampled clusters in the ith trip.

If $\bar{W}_i$ is a constant, its estimate $\bar{w}$ will be given by $\bar{w} = \sum_i \sum_j \sum_k w_{ijk} / \sum_i \sum_j m_{ij}$. In practice, N and M_i will not be known and will be estimated by $\hat{N} = \frac{nW}{\sum^n W_i} = W/\hat{\bar{\bar{W}}}$; $\hat{M}_i = \frac{W_i}{\bar{w}}$ respectively, if $\bar{W}_i$ is a constant $= \bar{w}$ (say).

Ratio Estimates of Mean and Total

The ratio estimate of mean catch $(\bar{\bar{Y}})$ per cluster is

$$\hat{\bar{\bar{Y}}}_R = \frac{\sum_i^n M_i \bar{y}_i}{\sum_i^n M_i} \doteq \frac{\sum_i^n W_i \bar{y}_i}{\sum_i^n W_i} \tag{1}$$

where $\bar{y}_i = \sum_j M_{ij} \bar{y}_{ij} / \sum_j M_{ij} \cong \sum_j W_{ij} \bar{y}_{ij} / \sum_j W_{ij}$.

The ratio estimate of total catch Y is

$$\hat{Y}_R = \frac{W}{\bar{w}} \hat{\bar{\bar{Y}}}_R. \tag{2}$$

The above estimators recommended for use are not workable in rockfish sampling because the sampler failed in almost all cases to subsample from more than one category in a sampled trip as would be seen from a sample of basic data for 1982 (Table 1) available for Eureka from the Department of California Fish and Game. The reasons for failure to collect the data are discussed in the section on Collection of Representative Data-Measurement Errors. The above estimators are, however, recommended for use in situations where the problem does not exist and, in particular, for single species where the categories are based on size. The estimates of error are given in Equations (4) and (5).

TABLE 1.—Distribution of landing weights (lb) from all categories and from the sampled category for Eureka for 1982.

Sample no. (boat trip)	Number of clusters sampled (m_i)	Market category sampled[1]	Weight of all fish (W_i) in a given trip	Weight of all fish for the category in a given trip
1528	1	269	26,550	24,176
1529	1	250	4,133	445
1530	2	269	59,218	58,239
1531	1	269	20,511	15,987
1533	1	269	35,022	14,661
1534	1	269	20,757	20,705
1535	1	269	15,812	8,436
1536	1	250	1,975	1,010
1537	1	250	16,055	1,075
1541	3	269	65,837	65,837

[1] Shows the code number of categories which are based on species, size, and quality.

Note: In all cases, only one of the categories could be sampled from a given trip. In boat 1541 there was only one category (269) of fish.

Estimation Ignoring Category Variation Within Sampled Trips

Assume that a cluster is selected at random from all possible clusters in a sampled trip. In other words, we ignore categories altogether both in sample selection as well as in estimation. Valid ratio estimates $\hat{\bar{\bar{Y}}}_{1R}$ of $\bar{\bar{Y}}$ and $\hat{Y}_{1R}$ of Y are respectively given by

$$\hat{\bar{\bar{Y}}}_{1R} = \frac{\sum_i^n W_i \bar{y}_i}{\sum_i^n W_i}; \; \hat{Y}_{1R} = \frac{W}{\bar{w}} \hat{\bar{\bar{Y}}}_{1R}. \tag{3}$$

Note these equations are essentially the same as Equations (1) and (2) except that we now assume that a cluster is randomly selected from all possible clusters in a sampled trip where W_i is the total landing weight from all categories for the ith boat trip in the sample ($W = \sum_i W_i$). In practice, the sampler would tend to subsample from a category which is accessible and is preponderant. This may lead to some bias in the estimate though its contribution to the total error will be negligible, since this would occur at the second stage of sampling.

The estimates of variance of estimated total and mean are approximately given by

$$v(\hat{Y}_{1R}) \doteq \left[\frac{1}{n} (1 - f_1) s_b^2 + \frac{f_1 (1 - \bar{f}_2) s_w^2}{n \bar{m}} \right] \left(\frac{W}{\bar{\bar{w}}} \right)^2 \tag{4}$$

$$v(\hat{\bar{\bar{Y}}}_{1R}) \doteq \left(\frac{\bar{w}}{W} \right)^2 v(\hat{Y}_{1R}) \tag{5}$$

$$\text{where } s_b^2 = \sum_i^n \left(\frac{W_i}{\hat{\bar{\bar{W}}}} \right)^2 \frac{(\bar{y}_i - \hat{\bar{\bar{Y}}}_{1R})^2}{n - 1};$$

$$s_w^2 = \sum_i^n \frac{\bar{m}}{n} \left(\frac{W_i}{\hat{\bar{\bar{W}}}} \right)^2 \frac{s_{2i}^2}{m_i} \tag{6}$$

and $s_{2i}^2 = \sum_k^{m_i} (y_{ik} - \bar{y}_i)^2/(m_i - 1)$; $\hat{\bar{W}} = \sum^n W_i/n$;

$$f_1 = \sum^n W_i/W; \bar{f}_2 = \frac{\bar{w} \sum_i^n \frac{m_i}{W_i}}{n}. \tag{7}$$

We will consider an operationally feasible plan in which sample trips at a port during a month are poststratified into categories and clusters are subsampled from each category; where one or more categories are missed due to inadequate field staff and/or management problems, clusters should be selected from other boat trips containing the missed categories.

Assuming that the cluster weight of the unequal cluster size varies over trips, i.e., $\bar{w}_i = \sum_j \sum_k w_{ijk}/\sum_j m_{ij}$ estimates of mean and total are

$$\hat{\bar{\bar{Y}}}_{2R} = \frac{\sum_i^n W_i\hat{R}_i}{\sum_i^n W_i/\bar{w}_i}; \hat{Y}_{2R} = W \frac{\sum_i^n W_i\hat{R}_i}{\sum_i^n W_i} \tag{8}$$

where $\hat{R}_i = \frac{\bar{y}_i}{\bar{w}_i}$; $v(\hat{Y}_{2R})$ and $v(\hat{\bar{\bar{Y}}}_{2R})$ can be obtained similar to Equations (4) and (5).

Estimation Based on Categories as Domains of Study

This method is almost as precise as proportional stratified sampling if within each port-month stratum (a) a minimum of four landings or boat trips ($n_j \geqslant 4$) is selected for each category and (b) the landing weights are available by categories after the season to serve as weights at the estimation stage. The minimum number in (a) is mainly based on limitations of field staff and budget restrictions. The ratio estimates of mean catch per cluster, total catch, and their errors, assuming clusters of equal size and using categories as domains of study are given by

$$\hat{\bar{\bar{Y}}}_{3R} \doteq \sum_j W_j\bar{\bar{y}}_j/\sum_j W_j; \hat{Y}_{3R} \doteq \sum_j \hat{Y}_j \tag{9}$$

$$\text{where } \bar{\bar{y}}_j = \sum_i^{n_j} W_{ij}\bar{y}_{ij}/\sum_i^{n_j} \mathrm{W_{ij}} \tag{10}$$

$$\hat{Y}_j = \bar{\bar{y}}_j \frac{W_j}{\bar{w}} \tag{11}$$

$$v(\hat{\bar{\bar{Y}}}_{3R}) \doteq \sum_j \frac{W_j^2}{W^2} v(\bar{\bar{y}}_j) + 2 \sum_j \sum_{<k} \frac{W_jW_k}{W^2} \operatorname{cov}(\bar{\bar{y}}_j, \bar{\bar{y}}_k) \tag{12}$$

and

$$v(\hat{Y}_{3R}) \doteq v(\hat{Y}_j) + 2 \sum_j \sum_{<k} \operatorname{cov}(\hat{Y}_j, \hat{Y}_k). \tag{13}$$

Both $v(\bar{\bar{y}}_j)$ and $v(\hat{\bar{\bar{Y}}}_{3R})$ are of standard forms and can be obtained as in Equation (4). Similarly, $v(\hat{Y}_j)$ and $v(\hat{Y}_{3R})$ can be obtained. The covariance terms in Equations (12) and (13) are ignored when the subsamples from different categories are from different boat trips and are, therefore, independent. In rockfish sampling this was found true, because the sampler failed in almost all cases to subsample from more than one category. In general, for all fish where sampling from more than one category per boat trip is feasible, e.g., with few species-size-qualities, Equation (13) should be used.

Assume that the clusters vary in size over trips. For any sort (say j)

$$\hat{Y}_{j_1} = \left[\sum_i W_{ij}\hat{R}_{ij}/\sum_i W_{ij}\right] W_j = \hat{R}_jW_j \tag{14}$$

and

$$\hat{\bar{\bar{y}}}_{j_1} = \sum_i W_{ij}\hat{R}_{ij}/\sum_i W_{ij}/\bar{w}_{ij} \tag{15}$$

$$\text{where } \hat{R}_{ij} = \frac{\bar{y}_{ij}}{\bar{w}_{ij}}; \hat{R}_j = \sum \hat{R}_{ij}W_{ij}/\sum_i W_{ij}. \tag{16}$$

If n_j is small compared to N_j and if the same subsampling strategy is applied to each of the sample landings, we have, ignoring contribution due to second-stage sampling units,

$$v_1(\hat{R}_j) = \frac{1}{n_j(n_j - 1)} \sum_i \left[\frac{W_{ij}}{\hat{\bar{W}}_{ij}}\right]^2 (\hat{R}_{ij} - \hat{R}_j)^2. \tag{17}$$

Another estimator $v_2(\hat{R}_j)$ is the jackknife

$$v_2(\hat{R}_j) \doteq \frac{(n_j - 1)}{n_j} \sum_i (\hat{R}'_{ij} - \hat{R}'_j)^2 \tag{18}$$

$$\text{where } \hat{R}'_{ij} = \frac{\hat{R}_{1j}W_{1j} + \ldots + \hat{R}_{(i-1)j}W_{(i-1)j} + \hat{R}_{(i+1)j}W_{(i+1)j} + \ldots + \hat{R}_{nj}W_{nj}}{W_{1j} + \ldots + W_{(i-1)n_j} + W_{(i+1)n_j} + \ldots + W_{n_j}} \qquad (19)$$

$$\text{and} \quad \hat{R}'_j = \frac{1}{n_j}\sum_i R'_{ij}.$$

Thus $\hat{R}'_{ij}$ is obtained by omitting trip i from the sample for sort j and calculating $\hat{R}_{ij}$ instead of $\hat{R}_{ij}$ as in Equation (16).

Hence, for category j of a species

$$v(\hat{Y}_{j_1}) = W_j^2 v_1(\hat{R}_j)$$

$$\text{or} \qquad = W_j^2 v_2(\hat{R}_j) \qquad (20)$$

where $v_1(\hat{R}_j)$ and $v_2(\hat{R}_j)$ are given by Equations (17) and (18).

For estimate of total over all sort groups for a species

$$\hat{Y}_{4R} = \sum_j \hat{Y}_{j_1} \qquad (21)$$

$$v(\hat{Y}_{4R}) = \sum_j v(\hat{Y}_{j_1}) + 2\sum_j \sum_{<k} \operatorname{cov}(\hat{Y}_{j_1}, \hat{Y}_{k_1}) \qquad (22)$$

A simpler formula $v(\hat{Y}_{4R}) \doteq \sum_j v(\hat{Y}_{j_1})$ can be used where subsamples from different categories are from different boat trips and are, therefore, independent.

It is, however, more reasonable to assume that the frequency distribution of fish caught is more uniform within a category so that cluster weight would be approximately a constant within a category. If so, the estimates of mean and total are given by

$$\hat{\bar{\bar{Y}}}_{5R} = \sum_j W_j \bar{\bar{y}}_j / \sum_j W_j; \; \hat{Y}_{5R} = \sum_j \hat{Y}_j \qquad (23)$$

$$\text{where } \bar{\bar{y}}_j = \sum_i W_{ij}\bar{y}_{ij} / \sum_i W_{ij};$$

$$\hat{Y}_j = \frac{\sum_i W_{ij}\bar{y}_{ij}}{\sum_i W_{ij}} \; \frac{W_j}{\bar{w}_j} \qquad (24)$$

and $\bar{w}_j$ is the simple mean weight of clusters in the jth group. Where the assumption of constant cluster weight within a category is not valid, the more general results given in Equations (14) and (15) should be used.

Comparison of Methods: Ignoring Category Variation Versus Poststratification by Categories

We will compare the efficiency of the estimators (3), ignoring variation due to categories, with the estimators (9), based on poststratification of landings by categories at a port during a month. The analyses were based on Eureka and Monterey data for 1982. The coefficients of variation (c.v.) of mean catch per cluster for a species based on categories as domains of study (method 2) were in almost all cases lower (Table 2) than ignoring category variation (method 1). Since method 1 results in underestimation of c.v.'s because sampling is actually based on a stratified random sample instead of a simple random sample, the increased precision of method 2 is all the more striking.

The c.v. of the estimated mean catch by sex-age groups for a species for which the number of sample landings were ≥10 (Table 3) were in all cases less for method 2 than for method 1. It may, however, be pointed out the c.v.'s are likely to be affected by factors such as growth, maximum age, and maximum size of fish. These have not been considered in this study. Thus, estimates based on categories as domains of study proved more efficient than ignoring categories altogether. Besides, method 2 has the added advantage of providing estimates by

TABLE 2.—Coefficient of variation (c.v., in percent) of mean catch by species at Eureka and Monterey based on the two methods during 1982.

Location and species	Sample size (number of boat trips sampled)	c.v. (%)	
		Method 1[1]	Method 2[2]
Eureka			
Widow rockfish	88	11.48	7.33
Chilipepper	88	30.83	32.12
Bocaccio	88	26.01	24.40
Monterey			
Widow rockfish	54	18.31	6.62
Chilipepper	54	15.68	13.92
Bocaccio	54	12.57	10.32

[1] Method 1, based on random categories (i.e., ignoring stratification by categories).

[2] Method 2, based on categories as domains of study.

TABLE 3.—Coefficient of variation (c.v., in percent) of mean catch by species-sex-age[1] group at Eureka and Monterey based on the two methods during 1982.

Eureka					Monterey				
Number of boat trips sampled	Sex	Age (yr)	c.v. (%) Method 1	c.v. (%) Method 2	Number of boat trips sampled	Sex	Age (yr)	c.v. (%) Method 1	c.v. (%) Method 2
				Widow rockfish					
17	M	7	19.71	18.83	10	F	13	39.98	24.29
18	F	7	13.50	10.94	10	F	12	35.16	20.49
				Chilipepper					
11	F	13	39.98	24.89	24	F	9	18.48	7.63
11	F	12	34.77	31.21	21	F	7	22.09	9.81
				Bocaccio					
15	M	6	30.10	19.82	14	M	7	27.46	12.45
19	F	6	35.87	32.45	20	F	7	24.34	10.06

[1] Age-sex groups for which primary sampling units (landings) are ≥10.

market categories which is of considerable economic importance.

COST FUNCTION

Consider the cost function

$$C = c_1 n + c_2 n \bar{m} \tag{25}$$

where c_1 is the average cost (in minutes) per boat trip due to transport, contact, and delay in making a contact, c_2 the average cost in data collection (identification of species, sex, length, otoliths, etc.) per cluster within clusters per boat trip and C is the total cost involved in visiting the primary sampling units (boat trips) and collecting data from the n boats with an average of $\bar{m}$ clusters per boat sampled. Data collected at Tiburon by the California Department of Fish and Game and the National Marine Fisheries Service show that c = 111.80 min, c_2 = 58.3 min so that $\frac{c_1}{c_2} = 2$ apply. However, from more recent studies conducted $\frac{c_1}{c_2} = 3$.

The components c_1 and c_2 were estimated at

Activity	*Percent*	*Mean (in minutes)*
Transport	50.0	81.7
Contact	5.0	8.7
Delay (off loading, etc.)	13.0	21.4
	68.0	111.8

Data collection	*Percent*	*Mean (in minutes)*
Species[1]	7.7	14.0
Sex, length	5.8	10.6
Otolith	10.8	19.7
Preparation time	7.7	14.0
	32.0	58.3

---

[1] Excluding samples dominated by single species.

Minimizing Equation (4) subject to Equation (25) for the optimum allocation we have

$$\bar{m}_{\text{opt}} = \frac{s_w}{\sqrt{s_b^2 - \dfrac{s_w^2}{\bar{m}}}} \sqrt{\frac{c_1}{c_2}}\,. \tag{26}$$

TABLE 4.—Optimum values of *m* for estimating species catch per cluster by categories for different variance and cost ratios, 1978.

Species	Category[1]	n	s_b^2	s_w^2	$\bar{m}$	m_{opt}	
						$c_1/c_2 = 2$	$c_1/c_2 = 3$
Eureka							
Bocaccio	250	25	1.80	3.01	2.16	3.86	4.73
Chilipepper	250	13	24.45	3.13	1.92	0.52	0.64
Widow rockfish	250	11	59.49	8.71	2.46	0.56	0.68
Monterey							
Bocaccio	253	31	95.15	4.20	1.97	0.63	0.77
Chilipepper	253	33	43.71	4.16	1.94	0.45	0.55
Widow rockfish	253	12	22.38	4.66	2.00	0.68	0.84

[1] Code numbers of categories which are based on size, species and quality.

The variation among clusters (s_b^2) in different landings at Eureka and Monterey for 1978 was in almost all cases greater than between clusters within the same landings (Table 4); also the optimum number of clusters per boat for estimating species number was mostly unity. Data from other ports follow the same pattern. Since a minimum of two clusters is needed to provide an estimate of between cluster within trip variation, a subsample of two clusters per category per trip is recommended. In practice, it is preferable to select a systematic sample of clusters separated in time.

VARIANCE COMPONENTS: SPECIES-AGE AND LENGTH GROUPS

A two-level nested analysis of variance for length and age with unequal sample size for species based on sample landings at ports during 1979 (Table 5) shows that both the variation, because of length and age, was generally high among sample landings compared with clusters within landings. Also, variation between clusters was generally of the same order as within clusters, and the optimum number of clusters was ≤2. Data for other ports and years (not shown in the table) mostly supported the findings.

On the whole, both the variation in species number (Table 4) as well as in length and age (Table 5) was consistently high among sample landings relative to between clusters within landings; also, variation among clusters was not significant compared with variation within clusters. Hence, for precise estimation of species number, length, and age composition for a category at a port during a season, data should be collected from a large number of landings and from few clusters (two) from a category within a sample landing.

RELATIVE EFFICIENCY OF ESTIMATORS USING POSTSTRATIFICATION

Consider the three estimators of total catch for a sort of a species at a port during a year. We will use the same selection procedure with poststratification by sorts but different estimation procedures.

$$\hat{Y}'_j = \frac{N_j}{n_j} \sum_{i=1}^{n_j} \bar{y}_{ij} \tag{27}$$

$$\hat{Y}_j = \frac{\sum_i^{n_j} W_{ij}\bar{y}_{ij}}{\sum_i^{n_j} W_{ij}} \; \frac{W_j}{\bar{w}_j} \tag{28}$$

$$\hat{Y}_{j_1} = \hat{R}_j W_j \tag{29}$$

where $\hat{R}_j$ is given by Equation (16), $\bar{y}_{ij}$ is the simple mean of species number per cluster for sort j from the ith sample, $\hat{Y}_j$ is the same as Equation (24) with a constant cluster weight within a sort group, and $\hat{Y}_{j_1}$ is a more general estimator based on the assumption that cluster weight varies among trips. For $v(\hat{Y}_{j_1})$ use $W_j^2 v_2(\hat{R}_j)$ where $v_2(\hat{R}_j)$ is the jack-

TABLE 5.—Two-level nested ANOVA of length and age of species with unequal sample sizes by ports during 1979. MS = mean square; F = F-RATIO, Statistic; P = observed probablity level.

	Age				Length			
Source	df	MS	F	*P*	df	MS	F	*P*
Widow rockfish at Eureka								
Samples	15	34.45	4.75	<0.005		37.86	3.09	<0.025
Clusters (within samples)	13	7.25	1.19	0.35		12.27	1.43	~0.18
Within clusters	320	6.09				8.58		
Chilipepper at Monterey								
Samples	43	31.74	4.05	<0.001	48	145.20	4.02	<0.001
Clusters	39	7.84	1.80	~0.001	44	36.10	1.43	~0.035
Within clusters	320	4.35			971	25.25		
Bocaccio at San Francisco								
Samples	10	84.97	6.95	<0.001	10	317.88	6.98	<0.001
Clusters	15	12.23	1.20	~0.30	16	45.55	0.80	~0.75
Within clusters	225	10.20			227	57.11		

knife estimator of Equation (18) and for $v(\hat{Y}_j')$ see Sukhatme (1954). $\hat{Y}_j'$ is generally subject to considerable bias.

The c.v. of total catch of bocaccio, chilipepper, and widow rockfish for different categories by port-year groups (Table 6) show that the estimators $\hat{Y}_j$ and $\hat{Y}_{j_1}$ are highly efficient compared with $\hat{Y}_j'$; also, $\hat{Y}_j$ turns out to be slightly superior to $\hat{Y}_{j_1}$ since the jackknife estimator $v_2(\hat{Y}_{j_1})$ is an underestimate and does not take into account the contribution of the within component of variance. Thus, the empirical evidence supports strongly the use of the estimator $\hat{Y}_j$.

TABLE 6.—Coefficient of variation (in percent) of estimates of total catch of bocaccio, chilipepper, and widow rockfish per cluster by ports during 1978 and for different categories for the three estimators $\hat{Y}_j'$, $\hat{Y}_j$, and $\hat{Y}_{j_1}$.

Port	Category	Number of boat trips sampled	$\hat{Y}_j'$	$\hat{Y}_j$	$\hat{Y}_{j_1}$
		Bocaccio			
San Francisco	253	20	13.51	10.24	11.64
Fort Bragg	250	86	16.21	7.36	8.14
Monterey	253	31	12.07	17.93	19.51
Eureka	250	25	40.11	26.00	29.84
		Chilipepper			
Eureka	250	13	37.66	34.52	42.33
		Widow rockfish			
Monterey	250	12	111.20	43.47	68.29
Eureka	250	11	72.69	27.81	33.90

AGE-COMPOSITION: DOUBLE SAMPLING

Studies mentioned in the Introduction section have shown that since aging from otoliths of each individual fish in a sample is more expensive than an easily measured quantity such as length, it may pay 1) to choose a random subsample from the whole sample of length measurements for age determination or 2) stratify the sample according to length classes and choose a subsample from each class for age determination. The technique is profitable only if the correlation between length and age is fairly high.

It may be recalled that considerable bias is introduced by applying age-length keys developed during a year to subsequent years. Both Kimura (1977) and Westrheim and Ricker (1978) showed that age-length keys can yield most inefficient estimates of numbers-at-age with substantial overlap of lengths between ages. In the latter case the correlation between length and age will be low for the larger and the very small sizes. Consequently, we will need a higher sampling intensity at the tails to provide reliable estimates of age for such sizes.

In the construction of length strata for selection of the subsample, additional questions arise on 1) number of strata to choose, 2) strata boundaries to decide, and 3) the number of sampling units to be allocated to each stratum for deriving maximum gain from double sampling. These are discussed as follows.

Number of Strata

The values of $V(\bar{y}_{st})/V(\bar{y})$ (Cochran 1977) are given below as a function of L, the number of strata using the linear model

$$y = \alpha + \beta x + \varepsilon \qquad (30)$$

where y is the length, x the age of female widow rockfish and

$$\frac{V(\bar{y}_{st})}{V(\bar{y})} = \frac{\rho^2}{L^2} + (1 - \rho^2) \qquad (31)$$

where ρ is the correlation between length and age in the unstratified sample and L the number of strata. It can be shown for this model that when $L \geqslant 6$ and $\rho > 0.95$, there is hardly any gain due to stratification (Table 7). The improvement in stratification is highest for data set 1 for which $\rho^2 = 0.7004$ and lowest for set 3 for which $\rho^2 = 0.5278$. The results for the regression model indicate that unless ρ exceedes 0.95, little reduction in variance is to be expected beyond $L = 6$. Data sets 1, 2, and 3 support this conclusion. In fact, there does not seem to be any profit resulting from increase in strata beyond $L = 5$.

Strata Boundaries

For the length-age strata on 239 females (widow rockfish) landed during 1982 at San Francisco and the rule based on the cumulative of $\sqrt{f(y)}$ (Cochran 1977) where y denotes the length in centimeters, the nearest available points for the two strata are

	Stratum 1	Stratum 2
Boundaries	36-47 cm	48-55 cm
Intervals on cum $\sqrt{f}$	18.70	23.72

TABLE 7.—$V(\bar{y}_{st})/V(\bar{y})$ as a function of L for the linear regression and for some actual data.

	Linear regression model ρ =				Data set		
L	0.99	0.95	0.90	0.85	1	2	3
2	0.265	0.323	0.392	0.458	0.4747	0.5114	0.6041
3	0.129	0.198	0.280	0.358	0.3774	0.4209	0.5308
4	0.081	0.154	0.241	0.323	0.3434	0.3892	0.5052
5	0.059	0.134	0.222	0.306	0.3276	0.3746	0.4933
6	0.047	0.123	0.212	0.298	0.3154	0.3740	0.4890
∞	0.020	0.098	0.190	0.277			

		Type of data		
Set	Data	x Age (yr)	y Length (cm)	Source
1	Female widow rockfish (532) Monterey, San Francisco and Bodega Bay	1982 (Jan.-Mar.)	1982 (Jan.-Mar.)	Department of California Fish and Game and Tiburon Laboratory
2	Female widow rockfish (444) Eureka	1981 (Jan.-Sept.)	1981 (Jan.-Sept.)	
3	Female widow rockfish (328) Eureka	1980 (Apr.-Dec.)	1980 (Apr.-Dec.)	

It turns out that the division point is approximately the same for young as well as old widow rockfish.

For length-age data (1981) based on 444 females (widow rockfish) landed at Eureka, the boundaries using 2 and 3 strata are

	Stratum 1	2
Boundaries	31.5-47 cm	46.5-55 cm
Intervals on cum $\sqrt{f}$	17.70	29.01

	1	*Stratum* 2	3
Boundaries	31.5-46 cm	46.5-49 cm	49.5-55 cm
Intervals on cum $\sqrt{f}$	17.70	13.12	15.89

Optimum Allocation Plan

Double sampling with regression is more efficient than single sampling (when the first sample is measured for age alone) for the same cost if

$$\rho^2 > \frac{4\frac{c}{c'}}{\left[1 + \frac{c}{c'}\right]^2} \tag{32}$$

where ρ is the correlation between length and age of fish, c and c' are respectively the costs of aging and measuring a fish. Assuming that the average cost of aging a rockfish (including small and large fish) is 6 min and of measuring it is 1.2 min (estimates based on measurements by W. Lenarz of Tiburon Laboratory), we have from Equation (32)

$$\rho^2 > 0.5555$$

or

$$\rho > 0.7453.$$

For the three data sets (Table 7) the values of ρ^2 are respectively 0.7004, 0.6515, and 0.5278 so that Equation (32) is approximately satisfied. However, neither ρ nor $\frac{c}{c'}$ are large enough to suggest that double sampling will be much more efficient than single sampling.

We will illustrate the use of double sampling for stratification by analyzing 1981 length-age data at Eureka to estimate the proportion of female in age group 11, based on a sample of 444 fish. For the three length strata, h = 1, 2, 3 with stratum boundaries based quadratic fit of length on age are 31.5-43, 43.5-49, 49.5-55. (Note this is different than boundaries based on length only.) Also

$$c_0 = 1.2 \text{ min}, \; c_1 = 3.8 \text{ min}, \; c_2 = 3.8 \text{ min, and } c_3 = 8 \text{ min}$$
$$w_1 = 0.0653, \; w_2 = 0.5451, \text{ and } w_3 = 0.3896$$
$$s_1 = 0.1825, \; s_2 = 0.4966, \; s_3 = 0.1503,$$
$$\text{and } s = 0.4343$$

where w_1, w_2, and w_3 are the proportions of fish in the sample, c_0 is the cost of measuring a fish and c_1, c_2, c_3 are respectively the costs of aging them in the three length groups. From Cochran (1977, p. 331) we have

$$v_{\min}(p_{st}) = \frac{1}{C^*}\left[\sum w_h s_h \sqrt{c_h} + (S^2 - \sum w_h s_h^2)^{1/2} \sqrt{c'}\right]^2 \qquad (33)$$

$$= 0.8915/C^*$$

where p_{st} is the estimated proportion and $C^* = E(c) = E(c_0\, n + \sum_n c_h n_h)$ with $n_1 = 14$, $n_2 = 120$, $n_3 = 48$ and $n' = 444$. The efficiency of double sampling with respect to single sampling is given by

$$v_{srs}(p)/v_{\min}(p_{st}) = 1.27$$

where $v_{srs}(p) = 0.1885/\frac{C^*}{6}$, i.e., double sampling is 27% more efficient than single sampling. However, as noted by Ricker (1975) the increase in accuracy achieved by combining a length sample with a smaller age sample may not be great unless fish used for age determination is taken from the same stock, during the same season and using gear having the same selective properties as the length-frequency samples. This point will generally be met if fish are subsampled systematically for age from fish arranged in increasing (or decreasing) order of length from a port-month stratum. Our studies have shown that the best length-age fit does not change significantly if age determination is made on every other fish arranged in ascending order of length.

It is difficult to obtain reliable estimates of the numbers at age for the extremely small or larger sizes because lengths cannot be used for estimating age. There is need for search for other auxiliary variables (other than length) associated with age and for increase in sampling rate at the tails. In double sampling where lengths are obtained in the first phase, a number of small clusters may be used separated in space and time to provide a large number of fish at the tails for estimating numbers at age. The extent of bias in estimation of numbers at age through length-age key approach may be tested by Monte Carlo simulation.

COLLECTION OF REPRESENTATIVE DATA-MEASUREMENT ERRORS

Owing to uncertainty of arrival times and varying unloading procedures, no objective method is available to ensure random sampling of the trips. When the vessels return to port, they are usually available for sampling except when they are transhipped immediately due to inclement weather, lack of processing facilities, uncooperative buyers, or unscheduled deliveries at short notice. It is, however, not unreasonable to regard a set of sample landings during a week at a port as random and representative of the totality of all landings at the port for the month.

Although rockfish are landed by categories, which are mostly determined by market agreement based on size, composition, and condition of the catch, the number of categories per delivery cannot be predetermined. This number would vary from delivery to delivery and from dealer to dealer. Also, there are no guarantees that a complete boat sample, covering clusters from each category, can be taken on any sampling day and some of the categories are actually missed in sampling. Some of the possible reasons for missing the categories are 1) when landing weight would not occur during regular hours, one of the sorts may have already been shipped before the sample could arrive at the spot; 2) often one of the sorts may be quite small and there may be a buyer at the dock waiting for the fish to be taken away; 3) while the sampler is working on a sort, the other sort(s) will have either been processed or shipped away; and 4) the sampler may be prevented from taking a sample from another sort by the skipper who may not like some of his fish being cut and otoliths removed for biological studies. This may happen at ports where either processing facilities are inadequate or fish are bought by local merchants immediately after landing. The question arises if failure to sample from all categories of a sample landing as originally planned would cause appreciable bias and loss in efficiency in the estimates of species catch and its distribution and whether a more efficient method could be developed that is operationally feasible. This point has been examined in the present paper.

The present technique of selecting a cluster (box) of fish as second stage sampling unit is preferred to random selection of a specified number of individual fish because in practice the potential of personal bias of the sampler could be considerable. Often fish chosen by the latter technique are ones closest to the sampler or those that fell in a certain position. Tomlinson (1971) felt that in this approach the sampler may tend to choose a fish with certain qualities and thus may introduce procedural bias.

The selection of a representative cluster would depend whether samples after sorting on the vessel come from bins, strap boxes, or off conveyor belts. Buyers from small markets occasionally select fish from the top of bins. Hence, to avoid this bias, it is preferable to select the cluster from the conveyor belt which exposes unsorted fish from the lower portion of the bin. However, where small market buyers do not buy fish, a cluster may be selected from a bin. Where many bins are present a systematic sample of two clusters, preferably from the beginning and end of the trip may be selected. Where fish are graded on a conveyor belt before they enter the plant (e.g., Fieldslanding at Eureka) the sampler should try to intercept the landings prior to secondary sorting or obtain separate weights for each subsort category. In general, selection of a cluster for a market category should be done before any presorting is done at the port.

It has been pointed out earlier that bias may result from personal selection of fish within a cluster. If the sampler were to select a number of clusters with few fish per cluster, a cluster will on the average contain more big fish. This would lead to high nonsampling bias. Sometimes, the top few fish in a bin are selected and put there to impress small buyers. The resulting bias in selection can be avoided by taking all the fish in a cluster (e.g., 50 lb) from one side of the box.

For obtaining reliable and comprehensive information on population characteristics, it is essential for the sampler to maintain good relationships with both the skipper and the buyer; this will depend to a large extent on the expertise of the sampler gained in the course of the field work.

SUMMARY

1. The sampling scheme at a port during a month with poststratification of sampled trips into categories and subsampling of clusters from each category (see sections on Estimation with poststratification and Estimation ignoring category variation) is not workable for estimating rockfish catch since some of the categories may be missed in sampling due to inadequate field staff and/or management problems.
2. For other commercial fish where the above problem does not exist and landing weights by categories are not available at the end of the season, the methods (see sections on Estimation with poststratification and Estimation ignoring category variation) are recommended, e.g., for single species where the categories are based on size.
3. For estimating the catch of rockfish, a two-stage sampling plan is recommended with boat trips as first stage units poststratified into categories and clusters subsampled from a category; estimates are based on categories as domains of study with landing weights available for each category. A minimum of four landings or boat trips should be used for each category, to provide efficient estimates. With few categories, this number is likely to be large.

   Where only one category is subsampled for each boat in the sample, $v(\hat{Y}_{3R}) = \sum_j v(\hat{Y}_j)$. In all other cases Equation (13) should be used.
4. The design described in the above paragraph is recommended for use in other fisheries where landing weights are available for each category. Equations (9) and (21) are recommended for the estimation of catch according as the clusters are of equal or unequal size. Equations have been provided for the more practical case when cluster weight can be treated as constant within a category but different among categories.
5. Estimates of species catch by sex and age based on method 1 are less efficient than those based on method 2 which is based on categories as domains of study (Tables 2, 3).
6. Method 2 is preferred to method 1 when there

is variation among categories. This is true for all fish.

7. With few categories (species-size-qualities) the chance of missing a category is reduced. Equations (9) and (13) should be used for clusters of equal size and Equations (21) and (22) for unequal size clusters. This result is, of course, applicable to all commercial fish.
8. As far as practicable, selection of a cluster for a market category should be done before any presorting is done at the port either from bins, strap boxes, or off conveyor belts.
9. Variation (within categories) in length and age for a species was considerably higher among boat trips than among clusters within boat trips. Also, variation among clusters was not significant, compared with variation within clusters (Table 5). Hence, for precise estimation of species number, length, and age composition for a category at a port during a season data should be collected from a large number of landings and from few clusters from a category within a sample landing. This result should hold for all commercial fish.
10. For the cost function $C = c_1 n + c_2 n\bar{m}$ where c_1 is the average cost (in minutes) per boat trip due to transport, contact, and delay in making a contact, c_2 the average cost of data collection (identification of species, sex, length, otoliths, etc.) per cluster per boat trip and C is the total cost involved in visiting the primary sampling units (boat trips) and collecting data, the optimum number of clusters per sampled trip for a fixed cost for a category is two (Table 4). This should provide valid estimates of error as required in Equations (13) and (22).
11. The principal contribution of the paper is that a minimum of four sample landings be subsampled for each category from a port-month stratum, i.e., about 1 per week and two clusters of 50 lb (25 lb for small fish) each should be sampled to provide port-year estimates with a reasonable degree of accuracy.

    If a category is infrequently landed, sampling should be directed towards the infrequent category, as long as the number of landings for the category is less than four per month.
12. The efficiency of the ratio estimator (Equation (28)) based on poststratification by categories at port-year level and using constant cluster weight within a category was compared with two other estimators, including the ratio estimator based on jackknife. Empirical evidence indicated that the ratio estimator using constant cluster weight within a category proved most efficient for estimation of species catch.
13. Age-length keys can yield most inefficient estimates of the numbers at age for extremely small and large fish. It is suggested that cluster sampling for length be based on a number of clusters separated in space and time; also, sampling for age should be intensified for small and large fish. This approach is applicable to all fish.
14. Double-sampling was adopted for estimating proportion of widow rockfish in 11-yr age group. A sample of fish was divided into 3 strata and optimum allocation for age was adopted within strata. The estimated proportion was 27% more efficient than if single sampling were adopted.

The best length-age did not change significantly if age determination is made on every other fish selected in ascending order of length.

The method is general and is applicable to all fish.

ACKNOWLEDGMENTS

Thanks are due to William Lenarz of Tiburon Laboratory for providing information on problems related to widow rockfish landings on the Californian coast, to Candis Cooperider and Mark Allen for the computations done on data collected, to the field staff of the California Department of Fish and Game responsible for collection of relevant data, and to Norman Abramson, Director, Tiburon Laboratory for all the assistance rendered to me during my work in the Laboratory. My thanks are also due to Pat Dalgetty, Department of Mathematics and Statistics, University of Calgary, for assistance in typing the paper and finally to the referees for helpful comments.

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8697

CARANGIDAE — Bigeye Scad

by Paul M. Shiota

Valid name	*Selar crumenophthalmus* (Bloch 1793) (Fig. 57)
Synonymy	*Scomber crumenophthalmus* Bloch 1793 *Caranx crumenophthalmus* Lacepède 1802 *Caranx mauritianus* Quoy and Gaimard 1824 *Caranx macrophthalmus* Rüppell 1828 *Trachurops crumenophthalmus* Gill 1863 *Selar mauritianus* Wakiya 1924 *Selar macrophthalmus* Wakiya 1924 *Trachurops mauritianus* Jordan and Hubbs 1925 (from Jordan and Evermann 1905; Williams 1958)
Common and vernacular names	Bigeye scad; paaa (5.1-7.6 cm); hahalalu (7.6-22.8 cm); akule (>22.8 cm)

Distribution

Distributed throughout the entire Hawaiian Archipelago. Found from Necker Island to Midway in the NWHI.

In the main islands, bigeye scad inhabit coastal waters of all islands from shoreline to depths of about 100 m (Kawamoto 1973; Kazama[11]) and form schools numbering from a few to tens of thousands of individuals.

Distinguishing characteristics

D. VIII+I, 25-27 (usually 26); A. II+I, 20-22 (usually 22); P1. I, 19-20; P2. I, 5; LLs. 81-95 of which 28-37 are modified into scutes; Gr. 10-11+27-28 (Schultz et al. 1953). Body oblong, moderately slender, typically mackerel-like. Eye diameter contained three times or less in head length; adipose eyelids well developed and extend to pupil, leaving the eye as a narrow slit; portion of pectoral girdle that forms posterior margin of gill opening has a deep furrow; teeth in both jaws uniseriate; vomer and palatines toothed; lower jaw projecting; maxillary of moderate width, ending under anterior margin of pupil; first dorsal fin high, spines connected by membranes; two anal spines well developed; pectoral fin reaching origin of soft anal fin, soft dorsal and anal fins slightly elevated anteriorly, fin bases equal in length; anterior portion of lateral line with a long low arch, becoming straight below middle of soft dorsal fin; scutes only on straight portion of lateral line.

In life, bluish to greenish silver on the upper third of the body and silvery white on the lower two-thirds. Attains a maximum size of about 38.0 cm (Gosline and Brock 1960); the majority range from 21.0 to 26.5 cm FL (Kawamoto 1973).

Life history

The species is relatively fast-growing. Bigeye scad is 10.2-17.5 cm when it first appears in shallow coastal waters in large schools and grows to 22.9 and 30.5 cm by the end of the first and second year, respectively. Results from tagging experiments indicate that akule is not migratory and tends to remain in very localized areas (Kawamoto 1973).

Bigeye scad is heterosexual without obvious external sexual dimorphism, has a sex ratio of 50:50 in mature adults, and is believed to be promiscuous (Kawamoto 1973). Spawning is pelagic and eggs are spherical, with a single oil globule, nonadhesive, and free-floating (Kawamoto 1973; Johnson 1978). Females reach sexual maturity and begin spawning at about 23.5-25.0 cm when they are 10-12 months old, and males mature at about 22.0-23.0 cm when they are about 8-9 months old (Kawamoto 1973).

Samples collected during NMFS cruises indicate that the reproductive cycle is seasonal in the NWHI, similar to that of bigeye scad in the main islands. Specimens collected at Kure Atoll and Midway in June were mature; whereas fish from Laysan Island, Maro Reef, French Frigate Shoals, and Necker Island were mature in July. Sampling at Nihoa and French Frigate Shoals in November produced a predominance of juveniles. This is in agreement with results of studies in the main islands where gonads were predominantly mature or spent in April-November (Kawamoto 1973), and fish under 15.0 cm appeared in shallow coastal waters in large schools in July-December (Gosline and Brock 1960). The evidence suggests that spawning occurs in the spring and summer (February-August).

The NMFS surveys have demonstrated that before spawning, mature fish move into shallow water, similar to spawning adults which form large schools in shallow, sandy, or flat-bottomed areas <22 m in the main islands (Gosline and Brock 1960). For example, at Midway, sampling in the lagoon in June in waters <3.6 m produced large numbers of bigeye scad with mature gonads. Similarly, schools of large bigeye scad with mature gonads occurred in July in shallow water on the leeward side of Laysan Island.

Although in the main islands juveniles are caught by recreational fishermen with pole and line during daylight, bigeye scad are primarily night feeders. The bulk of their diet is composed of small fishes such as anchovies and holocentrids, and crustaceans such as copepods, crab megalops, stomatopods, and shrimps (Kawamoto 1973). This indicates that the species feeds primarily in the water column.

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[11] Kazama, T. K. 1977. The "akule" fishery of Hawaii. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, Admin. Rep. 1H, 1977, 5 p.

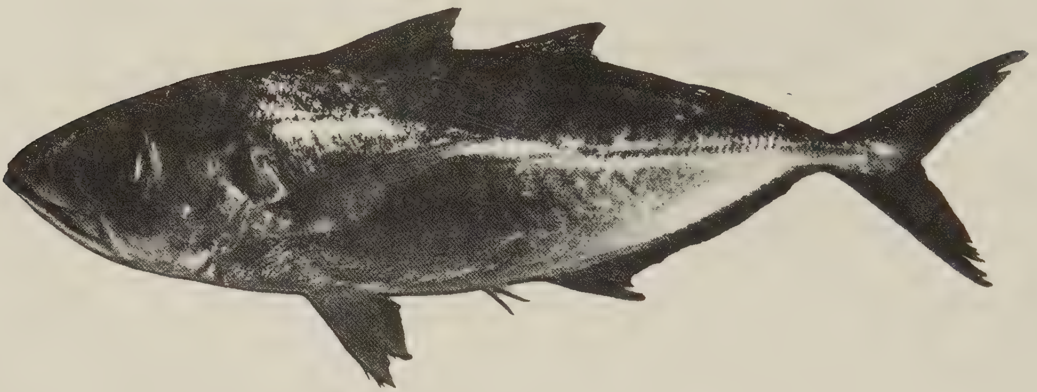


Figure 57.—*Selar crumenophthalmus.*

Gear and catch

In Hawaii, handlines, surround nets, and gill nets are the principal gear used to harvest bigeye scad. Handlining depends on the positive phototactic response of the akule (Powell 1968). Fishing is conducted at night from small boats in coastal waters to a depth of 100 m. The fish that accumulate under the light are jigged with a handline rigged with three to five baited hooks or artificial lures. Fishing is best during the new moon.

Landings of bigeye scad in Hawaii have fluctuated widely. From 1961 through 1979, the annual catch ranged from 68,342 to 444,556 kg and averaged 276,404 kg.

Presently, harvesting of bigeye scad occurs only in the main islands, although NMFS surveys have demonstrated the presence of large concentrations of this species at Necker Island, French Frigate Shoals, and Maro Reef. For the immediate future, it is unlikely that this species will be commercially harvested in the NWHI since there are adequate stocks in the main islands in close proximity to Honolulu where the largest demand for fresh fish exists.

8698

CARANGIDAE — Mackerel Scad

by Paul M. Shiota

Valid name	*Decapterus macarellus* (Cuvier and Valenciennes 1833) (Fig. 53)
Synonymy	*Caranx macarellus* Cuvier and Valenciennes 1833 *Caranx pinnulatus* Eydoux and Souleyet 1842 *Decapterus canonoides* Jenkins 1903 *Decapterus pinnulatus* Jordan and Evermann 1905 *Decapterus sanctae-helenae* Fowler 1928 (primarily from Norman 1935)
Common and vernacular names	Mackerel scad; opelu; opelu mama

Distribution

Present in large numbers around the main islands. Captured from Nihoa to Kure Atoll in depths from 22 to 38 m.

Distinguishing characteristics

D. VIII-I, 32-33-I; A. II-I, 28-29-I; scutes 20-25; LLs. 100-116. Body oblong, little compressed, almost perfectly fusiform; head moderate, pointed; mouth rather small, slightly oblique; jaws equal; palatines toothless or with a single series of minute teeth; no vomerine teeth; a small band of teeth posteriorly on tongue; adipose eyelid covering nearly entire eye; lateral line nearly straight from origin to interdorsal space, then descends until over fifth anal ray and continues straight to caudal fin (Jordan and Evermann 1905; Norman 1935).

Metallic bluish-black to bluish-green above and silvery white below in life. Small black spot near the upper margin of the opercle. Attains a length of about 50.0 cm (Gosline and Brock 1960).

During the NWHI surveys, three other *Decapterus* species were recorded. *Decapterus tabl* was easily separated from its Hawaiian congeners by its reddish tail. The other two species have yellow tails. *Decapterus macrosoma* has 28-30 rays on its anal fin and 25-30 scutes (Wakiya 1924; Berry and Smith-Vaniz 1978); *D. muroadsi* has 26-28 rays on its anal fin and 33 scutes (Wakiya 1924).

Life history

After hatching, the young fish remain in the pelagic environment, often forming large schools. Fishermen have reported schools of young fish as far as 80 nmi offshore.

Juvenile fish, 12.0-18.0 cm SL, first enter the coastal fisheries in late fall and winter. Once inshore, they grow at a fairly rapid rate, reaching 20.0, 27.1, and 30.7 cm SL after 12, 24, and 36 months, respectively (Yamaguchi 1953).

It attains sexual maturity by the end of the first year of life at about 18.0 cm SL. Spawning is in pelagic waters, in close proximity to its coastal habitat, from March-August, with a peak in May-July. Mature adults, 18.0 and 28.1 cm SL, have ovaries with approximately 83,000 and 212,500 eggs, respectively. Eggs are generally spherical, almost transparent, and contain a single shiny oil globule, which is 0.20-0.27 mm in diameter and is surrounded by tiny clusters of yolk granules (Yamaguchi 1953).

The species feeds heavily on zooplankton, mainly crustaceans, which comprised 94% of the total number of food items in the stomach (Yamaguchi 1953). Hyperiid amphipods and crab megalops were the most important among the crustaceans ingested. Thirteen of 24 stomachs examined by Yamaguchi also contained fish larvae. The stomach samples examined, however, may not reflect the true diet of opelu, because sampling was somewhat biased in that it was conducted under a night light which attracted phototaxic animals. It also did not account for possible seasonal and geographical differences in zooplankton abundance. For example, the diet of fish taken in Puerto Rico and the Virgin Islands was mainly pteropods (Randall 1967).

Gear and catch

An excellent food fish, mackerel scad is principally harvested commercially with hoop net and handline; gill nets and haul seines account for the remainder. In the late 1940's, hoop nets accounted for about 70% of the landings and handline the remaining 30%. However, in recent years (1971-78), the handline fishery accounted for a larger proportion of the landings (54%) compared with the hoop net fishery which produced only 39%.

In 1961-79, mackerel scad landings in Hawaii fluctuated between 77,874 and 194,143 kg and averaged 122,246 kg.

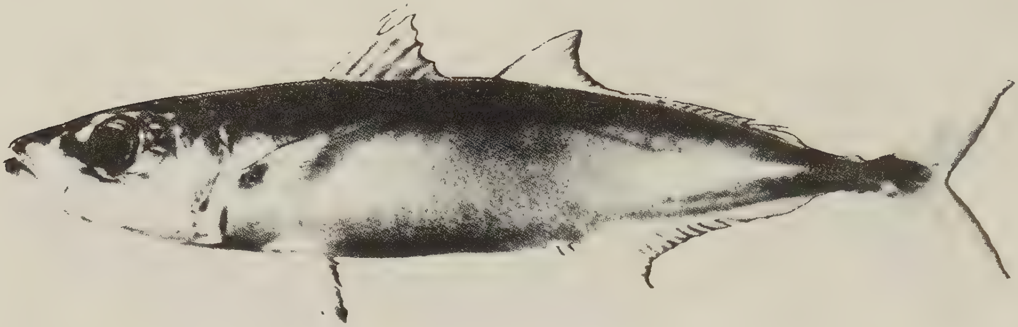


Figure 53.—*Decapterus macarellus*.

by Paul M. Shiota

Valid name	*Decapterus tabl* Berry 1968 (Fig. 54)
Synonymy	*Decapterus punctatus* Ginsburg 1952 (from Berry 1968)
Common and vernacular names	Redtail scad; redtail opelu

Distribution

This species was not recorded from the Hawaiian Archipelago until 1975 when a single specimen was caught at Necker in a bottom trawl in 393 m of water. Distributed in waters 18-393 m deep from Necker Island to Hancock Seamounts.

Distinguishing characteristics

D. VIII-I, 29-33; A. II-I, 24-26-I; LLs. 103-119; Gr. 10-12+30-33. Body rounded, elongate, slender; eye moderate; adipose eyelid well developed; teeth minute, in a single row in both jaws, becoming reduced in number and extent with growth; dorsal fins well separated; terminal ray of dorsal and anal fins consisting of a widely detached finlet; pectoral fins short; scales small, cycloid; lateral line arched to beneath the 13th to 16th dorsal soft ray; scales in curved part of lateral line 61-78, no scutes in curved part; anterior scales in straight part 0-8, scutes in straight part 34-44; dorsal accessory lateral line short, terminating near end of head; shoulder girdle with 2 slight papillae and a shallow groove above and below the pair, the lower papillae and groove the larger; vertebrae 10+14 (Berry and Smith-Vaniz 1978).

In life, metallic bluish-green to bluish-black above and silvery white below; tail reddish. Opercle with a small black spot near the upper edge. Largest Hawaiian specimen, taken at Hancock Seamounts, measured 42.8 cm FL.

Life history

Nothing is known about the life history of redtail scad in Hawaiian waters. In the Philippines juvenile fish in their second year of life enter the fishery in January-April; the bulk of the commercial landings, which consists of young maturing fish, is made in March-May (Tiews et al. 1970). As the fish begin to reach maturity in October-May during their third year of life, they exit the fishery for spawning grounds offshore (Tiews et al. 1970; Ronquillo 1972).

In the Philippines, spawning of *D. tabl* is slightly later than that of *D. macrosoma* which spawns between October and April (Magnuson 1970). Spawning occurs in the pelagic environment, the number of eggs spawned per fish ranging from 28,700 to 48,700 (Tiews et al. 1970).

Redtail scad feeds primarily in the water column on plankton such as copepods, mysis stages of crustaceans, and small fishes (Tiews et al. 1970).

Gear and catch

Red tail scad is harvested with mackerel handline, deep-sea handline, and bottom trawl. Catches up to 450 kg have been made with a fish trawl. There is no commercial fishery for this species in Hawaii.

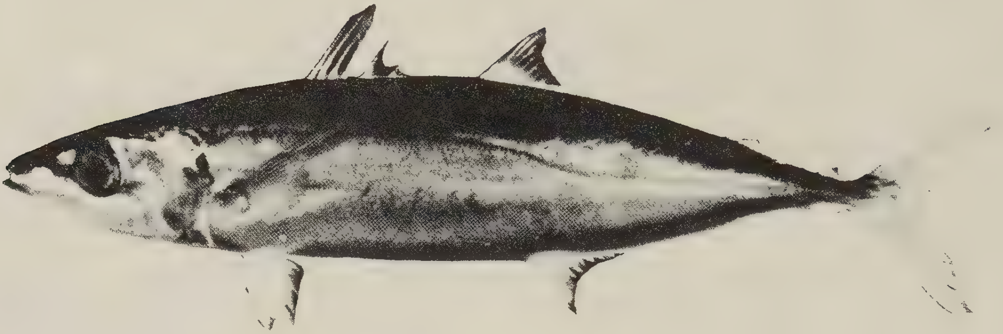


Figure 54.—*Decapterus tabl*.

86100

by Richard S. Shomura

■ Maka, a 2-year-old male Hawaiian monk seal, has received much attention lately because the National Marine Fisheries Service (NMFS) plans to move Maka from the Waikiki Aquarium to Sea Life Park to continue NMFS monk seal research. The purpose of this research on captive seals is to help save the Hawaiian monk seal from extinction. Dr. Leighton Taylor, director of the Waikiki Aquarium, is opposed to removal of the two NMFS monk seals from the Aquarium. Some of the recent media coverage of the issue based on a press release issued by Dr. Taylor gives an incomplete picture of the problem and situation.

Recently a meeting involving officials from the aquarium, the University of Hawaii and NMFS was held at the Honolulu Laboratory in an attempt to resolve the problem. Dr. Taylor, who is currently traveling on the mainland, was represented at the meeting by acting aquarium director Bruce Carlson. Others from the aquarium included Reid Withrow, a seal specialist, and Wayne Gocke, a member of the Waikiki Aquarium Board and an active volunteer worker at the aquarium. NMFS was represented by Richard S. Shomura, director of the Honolulu Laboratory, and William G. Gilmartin, head of the Marine Mammals and Endangered Species Program of the laboratory. Dr. Phil Helfrich, director of the Hawaii Institute of Marine Biology, chaired the meeting at the request of Dr. David Yount, University of Hawaii vice president for research. The aquarium is operated by the university, and Dr. Taylor reports to Dr. Yount.

Richard Shomura reported that "an agreement was reached in which Nuka (the older of the two seals at the aquarium) would remain at the aquarium for research, which would be within the guidelines established by the aquarium. This was a considerable concession by NMFS, since it reduced the research capabilities of the laboratory. Maka, the younger of the two seals, would go to Sea Life Park, with our (NMFS) assurance to the aquarium staff that we would have the details of a modified research plan reviewed by the NMFS Permit Office."

Shomura added, "The aquarium representatives were satisfied that the planned research was necessary and that this final approval of the new procedure would assure minimal risk to Maka."

Before a joint press release could be issued, Taylor called Helfrich to say that the agreement and the press release were unacceptable to him.

In reviewing the research to be conducted on Maka, Gilmartin emphasized that "the research involving Maka is high priority if we are to find out what is causing the deaths of several dozens of Maka's cousins at French Frigate Shoals annually. Young seals at French Frigate Shoals are experiencing a significantly higher mortality than at any other breeding island in the Northwestern Hawaiian Islands chain, and the cause may relate to availability of food. The experiment with Maka was to develop procedures to determine how efficiently monk seals feed in the wild. The double-labeled water technique, which Taylor objects to, is a standard procedure used by biologists on a number of wildlife including other species of seals."

Gilmartin further stated that "since the death of Tuffy, we have modified the test procedure and are confident that the study will present no more risk to the seal than force-feeing and collecting blood samples from Maka. Both procedures have been performed previously at the aquarium on Maka as well as on several other monk seals."

Shomura added that while he "believes this type of research is fully covered by our Federal Endangered Species Act Permit, our plans are to postpone the work until a fully detailed research outline has been reviewed by the NMFS Permit Office in Washington, D.C." Shomura expressed "surprise at Taylor's negative reaction to the research since Taylor was present when details of the research were given to the Hawaiian Monk Seal Recovery Team by Dr. Causey Whittow of the University of Hawaii in December 1984." Dr. Taylor is a member of the recovery team.

Shomura and Gilmartin believe NMFS has made a major concession in leaving Nuka at the aquarium and that, in taking Maka under the conditions mentioned earlier, they have satisfied most of the concerns for the safety of the animal voiced by the aquarium staff at the recent meeting.

Gilmartin said, "Maka will be moved at our earliest convenience for adaptation to the Sea Life Park facility and continuation of training for an audiogram study. While this research work is the only justification for keeping this endangered seal in captivity, public display will continue to be as much a part of Maka's life as possible, as it was at the aquarium." . . . . **Richard**

86101

SEAMOUNTS: A BIOLOGICAL CONCOURSE IN THE OPEN SEA
An Introductory Statement

RICHARD S. SHOMURA
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96822-2396

In 1883, Sir Thomas Huxley expressed a view that river fisheries can be exhausted by man, but the seas held almost unlimited supplies of food (Foster and Lankester 1903). He noted that the important marine resources such as cod, herring, and mackerel were inexhaustible. A caveat in his inaugural address, which was given at the Fisheries Exhibition in London in 1883, was that these resources were inexhaustible ''. . .in relation to our present modes of fishing.'' In the late 1800's it was not difficult to view the sea resources as very large and that man's fishing effort would only contribute a small fraction to the total mortality. However, today, after 100 years of fisheries exploration and expansion in the world's oceans, we know that the resources are not inexhaustible and that they can be overfished. Classic examples include the Peruvian anchovy and the Pacific sardine.

While history is proving Sir Thomas Huxley wrong on man's impact on the sea resources, his views on management of the river resources are certainly applicable to the high seas resources. He noted that river resources which have been exhausted by man's exploitation can usually be prevented because man's operations can be controlled. Thus, to optimize our harvest of the ocean resources we need to understand the dynamics of the system. This draws us to the reasons which led us to organize this workshop, ''Environment and resources of seamounts in the North Pacific.''

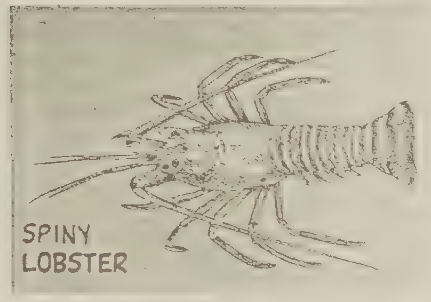
The bulk of the world's ocean resources comes from the coastal zones and the adjacent continental shelf. A small fraction comes from the pelagic areas and includes species such as the tunas, billfishes, sharks, and offshore squids. Until the 1960's seamounts were not considered of any consequence in fisheries. This changed in the late 1960's when Soviet trawlers were reported to land substantial quantities of finfishes from seamounts located in the central North Pacific (Sakiura 1972). A short while later references to a ''phantom'' fish began appearing in Japanese fisheries trade publications. These fish, whose scientific identity could not be ascertained because they were gutted and gilled at sea, were being caught by Japanese trawlers operating in the mid-Pacific. In the United States of America we were puzzled by the Soviet trawler activity in the waters just beyond the Hawaiian Archipelago and by the reports of ''phantom'' fish appearing in Japanese markets. Enlightenment on the subject came about during a talk given in Tokyo by Dr. Tokiharu Abe in 1970 when he described the ''phantom'' fish as the armorhead, *Pentaceros richardsoni* (= *Pseudopentaceros wheeleri*) (Abe 1972). Based on Dr. Abe's report it became apparent that the seamounts were the focus of a new fishery. Of interest is that until the development of the fishery, the armorhead was considered a rare species (Welander et al. 1957).

In comparison with the resources of the continental shelf and the open ocean, the seamounts are a direct source of only a small fraction of the world's marine catch. Details of the historical catch and present knowledge of seamounts will be presented during this workshop. It will suffice at this time to provide a brief description of seamounts.

A seamount is defined as an elevation rising 1,000 m or more from the sea floor, and of limited extent across the summit (U.S. Board of Geographic Names 1981). Although an accurate count of the number of seamounts in the Pacific is not available, the total number ranges in the tens of thousands (Scott and Rotondo 1983). Darwin suggested that the formation of islands, atolls and submerged reefs was the result of uplifting, subsidence, and coral growth (Hesse et al. 1937). Recent research in plate tectonics has provided the basis for a new explanation on the formation of seamounts (Scott

Identifying Characteristics of Hawai'i's Lobster

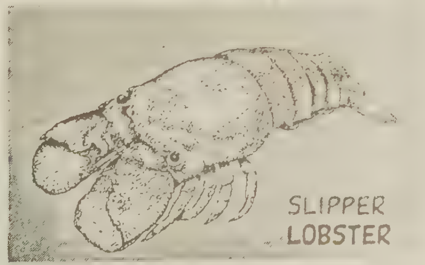
by Dr. Robert A. Skillman, Leader, Fishery Management Research Program, National Marine Fishery Service, Honolulu Laboratory.



Two species of spiny lobster and two slipper lobster occur in Hawai'i, but unfortunately none have commonly accepted Hawaiian or English names to differentiate them. One of the spiny lobster, *Panulirus marginatus*, is found only in Hawai'i and Johnston Island, while the other species, *Panulirus penicillatus*, is widely distributed throughout the Indo-Pacific.

These two species can be distinguished by examining the area between the eyes and antennae; *P. marginatus* has two main and several small spines while *P. penicillatus* has only four large spines. Another feature that distinguishes these species is the legs. Those for *P. marginatus* are solid colored while those for *P. penicillatus* have longitudinal white stripes. The color of *P. marginatus* is commonly brownish-red marbled with white, thus many people call it the red lobster; but it may also be purple, light yellow, or light brown. *P. penicillatus* varies in color from greenish- to reddish-brown, and it is sometimes called the green lobster.

The green lobster is found in shallow water, indeed on the reef in the breakwater, but it is not readily trapable. The red lobster occurs in shallow water, including in lagoons; but the commercial fishery, at least in the Northwestern Hawaiian Islands, occurs primarily from 15 to 35 fathoms. And, the red lobster readily goes into traps.



There is one species of slipper lobster that is commonly caught in Hawai'i's waters ranging from shallow lagoon areas to at least 35 fathoms. In fact, until 1984 *Scyllarides sguammosus* was thought to be the only slipper lobster occurring in Hawai'i. We now know that *Scyllalrides haanii* also occurs in Hawai'i, but is caught primarily at deeper depths, mostly 35 fathoms or deeper. The most obvious difference is that in *S. haanii* the tail section is strongly elevated or humped.

Spiny Lobster Fishery Analyzed

From the literature of the National Marine Fishery Service "Spiny Lobster Fishery Analyzed (Northwestern Hawaiian Islands)"

■ Fishery Management Research Program leader Dr. Robert A. Skillman, industry economist Samuel G. Pooley, statistician Gary L. Kamer and research assistant Wesley K. Higuchi analyzed the relationship between the carapace lengths and tail widths of the spiny lobster *Panulirus marginatus*. Analysis included tests to detect differences in samples between islands, sexes, and in functional forms.

The relationships were used by the spiny lobster planning team of the Western Pacific Regional Fishery Management Council to recommend a new size regulation for the Northwestern Hawaiian Islands' spiny lobster fishery.

The scientific and statistical committee of the council followed this recommendation and proposed the 5.1 cm tail width for the fishery; however, at its recent meetings in August, the council voted a smaller tail width (4.8 cm) based on economic considerations.

Dr. Skillman also reports that semiannual reports were prepared on the status of the NWHI spiny lobster fishery. Landings of spiny lobster have risen by 50 percent in the first half of 1985 (compared with the first half of 1984), but the amount of fishing effort (trap-nights) has increased substantially (45 percent). The effect is evident in a drop in spiny lobster catch rates.

At the same time, the targeting of slipper lobster by the fishery has increased the landings of these species dramatically (by 10 times). Midyear landings were 260,000 legal spiny lobster and 680,000 slipper lobster.

The spiny lobster planning team concluded that although the spiny lobster stock appears to be in reasonably good biological condition (the catches are within the maximum sustainable yield range projected by the fishery management plan), the declining catch rates and lower prices commanded by slipper lobster pose substantial commercial problems

Lobster Catch Rates

From a National Marine Fisheries Service press release on lobster fishing in the Northwestern Hawaiian Islands.

■ Catch rates at locations that are fished by Hawai'i's expanding lobster fishing fleet are noticeably lower than historical catch rates obtained by the National Oceanic and Atmospheric Administration research vessel *TOWNSEND CROMWELL* over five years ago, before extensive fishing began by commercial lobster boats. At Laysan Island, where there is no commercial fishery, catch rates were very similar to those obtained five years ago.

Fishery scientist Robert B. Moffit explained that two types of lobster traps were used by the *CROMWELL* to determine the current catch rate. Wire mesh traps that used to be the standard for the industry in Hawai'i had slightly better catches of large spiny lobster, while molded plastic traps, which are in current use by commercial vessels, had much higher catches of slipper lobster and small spiny lobster.

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Distribution of cetaceans and sea-surface chlorophyll concentrations in the California Current

R. C. Smith[1], **P. Dustan**[2], **D. Au**[3], **K. S. Baker**[4] **and E. A. Dunlap**[1]

[1] University of California Marine Bio-Optics, Department of Geography, University of California at Santa Barbara; Santa Barbara, California 93106, USA

[2] Department of Biology, The College of Charleston; Charleston, South Carolina 29424, USA

[3] National Marine Fisheries Service, Southwest Fisheries Center; La Jolla, California 92038, USA

[4] University of California Marine Bio-Optics, Scripps Institution of Oceanography, University of California at San Diego; La Jolla, California 92093, USA

Abstract

A census of marine mammals was conducted off the coast of California (USA) in 1979–1980. The distribution of sea-surface chlorophyll was determined at the same time by onboard fluorometry and by remote sensing using the Coastal Zone Color Scanner on the Nimbus-7 satellite. Comparisons of species and chlorophyll distributions indicate that marine mammals are not randomly distributed with respect to chlorophyll. Cetaceans were more abundant in the productive coastal waters than in the offshore oceanic waters of the California Current. This supports the hypothesis that the distributions of some cetacean species may be related to the mesoscale features that are manifest in the patterns of chlorophyll as revealed in the satellite imagery. It is suggested that oceanic chlorophyll may be used as a habitat descriptor for selected marine mammals, and that remote sensing will provide complementary data useful in the interpretation of observed distribution patterns of marine mammals and in the estimation of their abundance.

Introduction

The rich cetacean fauna off California, first described comprehensively by Scammon (1874), is the subject of increasing interest as human activities continue to intensify in coastal waters. Reviews (Norris *et al.*, 1976; Morejohn, 1977 a) have emphasized both the diversity and mobility of these cetacean populations within the California Current. This marine biome is well known for its rich biological production (Owen, 1974) due to upwelling and the mixing of surface water-masses (Reid *et al.*, 1958). Although one of the most intensively studied marine ecosystems in the world (Hickey, 1979), understanding of the extent and constitution of its cetacean fauna has remained sketchy. This is especially so beyond the continental slope, or off southern California, seaward of the borderland province (Shepard and Emery, 1941).

The work reported here began as two separate research efforts on board the same ship aimed at obtaining a census of marine mammals in the California coastal region and at obtaining surface-validation temperature and chlorophyll data over this broad area in support of satellite sensors. The surface data included the abundance and distribution of marine mammals from sightings and the continuous along-track recordings of near-surface temperature and chlorophyll concentration. The combined data sets allowed a quantitative evaluation of sightings with respect to the temperature and chlorophyll characteristics of the waters surrounding the sites where mammals were observed. The results demonstrate that cetaceans tend to be most abundant where chlorophyll is most concentrated. This is consistent with the hypothesis that cetacean habitats are primarily defined by the coastal, surface water-mass which is rich in chlorophyll, and that the mesoscale dynamics of these waters are important to the different cetaceans. It can further be hypothesized that the distribution of cetaceans is proximally related to the mesoscale distribution of primary productivity through links in the food web.

These ideas are not new. Whalers have long known that whales could be found where their food is plentiful (Foxton, 1956). In the Pacific, studies have shown that areas of mixing, upwelling, and frontogenesis frequently attract whales (Uda, 1954, 1962; Omura and Nemoto, 1955; Uda and Nasu, 1956; Uda and Dairokuno, 1957; Uda and Suzuki, 1958; Nasu, 1957, 1963, 1966; Rovnin, 1969; Volkov and Moroz, 1977; Berzin, 1978; Clarke *et al.*, 1978; Gaskin, 1982). The same appears true for the smaller dolphins and porpoises (Gaskin, 1968; Kasuya, 1971; Evans, 1974, 1975; Miyazaki *et al.*, 1974; Miyazaki, 1977; Miyazaki and Nishiwaki, 1978; Hui, 1979; Au and Perryman, in press). We suggest that if statistical relationships can be found between cetacean habitats, as distinguished by different temperature and/or chlorophyll regimes, then the spatial determination of these variables by remote sensors can quantitatively aid the estimation of abundance and distribution of marine mammals. While the data presented here were not obtained expressly for this purpose, the methodology discussed holds considerable potential for estimation of populations in the sea. Indeed, a main objective of this work is to suggest that combined ship and satellite sampling of the ocean may permit more quantitative assessments of living marine resources.

Both sea-surface temperature (Bernstein *et al.*, 1977; McClain, 1981; Bernstein, 1982; Brown and Evans, 1982) and chlorophyll concentration (Gordon and Morel, 1983) can now be quantitatively determined by satellite sensors. Sea-surface chlorophyll is related to the primary productivity of the water column to the depth of the euphotic zone (Smith, 1981), so that surface chlorophyll measurements may be used to estimate the distribution and amount of oceanic productivity (Smith *et al.*, 1982; Smith, 1984; Brown *et al.*, 1985; Eppley *et al.*, 1985). These data can be obtained from both ships and satellites, providing alternate and complementary sampling schemes. Satellite data are generally less accurate at single station points than those from ships, but provide almost real-time, synoptic coverage of large areas. The combination of ship and satellite sampling techniques permits a calibrated mapping of the regional distribution of sea-surface temperature and chlorophyll concentrations (Smith and Baker, 1982; Smith *et al.*, 1982; Brown *et al.*, 1985).

The purposes of the present work are: (1) to discuss the relative abundances and distributions of cetaceans and their relationships with ocean-water properties in California coastal waters; (2) to suggest methodologies for the utilization of synoptic satellite images (and the statistics derived therefrom) to optimize sampling strategies and improve abundance/distribution estimates of cetaceans.

This study focuses on the California Current, which brings cold subarctic water slowly southward along the California Coast. The current merges with tropical water around Latitude 23°N. Its western boundary, about 700 km from the coast, is the variable transition region between subarctic and Eastern North Pacific Central water. Seasonal coastal upwelling in spring and summer is driven by prevailing northwesterly winds. The major centers of upwelling occur at Latitude 41°N in the vicinity of Cape Mendocino, at Latitude 35°N off Point Conception, and at Latitude 28°N off Point Eugenia. Within the Southern California Bight, islands and irregular bottom topography contribute to locally intense, highly variable mixing and upwelling, which is intensified in the fall months by interaction with the seasonal Davidson Counter Current. Thus, while the California Current may be envisioned as a "wide body of water which moves sluggishly toward the southeast" (Sverdrup *et al.*, 1942), its local structure is characterized by highly variable swirls, eddies, and intermingling of water masses (Bernstein *et al.*, 1977; Hickey, 1979).

Reid *et al.* (1958) and Hickey (1979) have discussed the California Current system, its seasonal variability, and cross-shore structure which can be divided into nearshore (generally < 150 km) and offshore components. The nearshore region is primarily related to the seasonal fluctuation of wind-driven upwelling along the coast. The region offshore from the coast is more associated with the stronger southward flow of the California Current. For convenience, we frequently refer to the inshore component as "coastal" waters and the offshore component as "oceanic", but emphasize that both components are part of the California Current system. The coastal water tends to be chlorophyll-rich and is often differentiated sharply by fronts from the offshore, more oceanic water that grades into the core of the California Current. Both the oceanic boundary of this coastal water and the water mass itself are characterized by dynamic mesoscale features.

Materials and methods

A coastal marine mammal survey (Au and Duffy, 1979; Baker *et al.*, 1984) was conducted from the R. V. "David Starr Jordon" between 27 September and 20 October 1979 between Cape Mendocino and the tip of Baja California (see Fig. 1 for the northern portion of the survey area). A second marine mammal survey (Au, 1980) was made between 17 June and 11 July 1980, following a similar track pattern, but going south only to the latitude of Point Eugenia. There were additional legs on this cruise seaward of the previous September-October coverage, designed to investigate the effects of deep-sea seamounts on cetacean distribution.

Each day, the scientific crew searched continuously for mammals as the ship cruised in an offshore direction. They used 25 × 150 mm Fuji binoculars mounted port and starboard above the flying bridge. At night, the ship sailed to the shoreward start-point of the next day's leg. Along-track temperature and chlorophyll measurements were made continuously, 24 h a day. Vessel speed was between 9 and 10.5 knots (1 knot = 1.85 km h^{-1}). The observer's horizon was approximately 12 km away. Upon sighting a cetacean school, position, distance, and bearing information were recorded. Then the ship usually made a close approach for species identification, determination of school size, and behavioral observations.

Navigation and sighting fixes were provided by a Magnovox Satellite Navigational system with an accuracy of roughly one-half nautical mile. Along-track temperature, salinity and chlorophyll concentration data were recorded continuously on strip-chart recorders and sampled at 1 min intervals with a minicomputer (Hewlett Packard 9845). Temperature and salinity were recorded from the output of the onboard, calibrated thermosalinograph (Ocean Data Equipment TSG-102). Chlorophyll fluorescence was measured with a flow-through fluorometer (Turner Designs) and calibrated periodically with discrete extracts of chlorophyll (Smith *et al.*, 1981).

Satellite imagery from the Coastal Zone Color Scanner aboard the Nimbus 7 satellite (Hovis *et al.*, 1980) was captured at the Scripps Satellite Oceanography Facility. Image

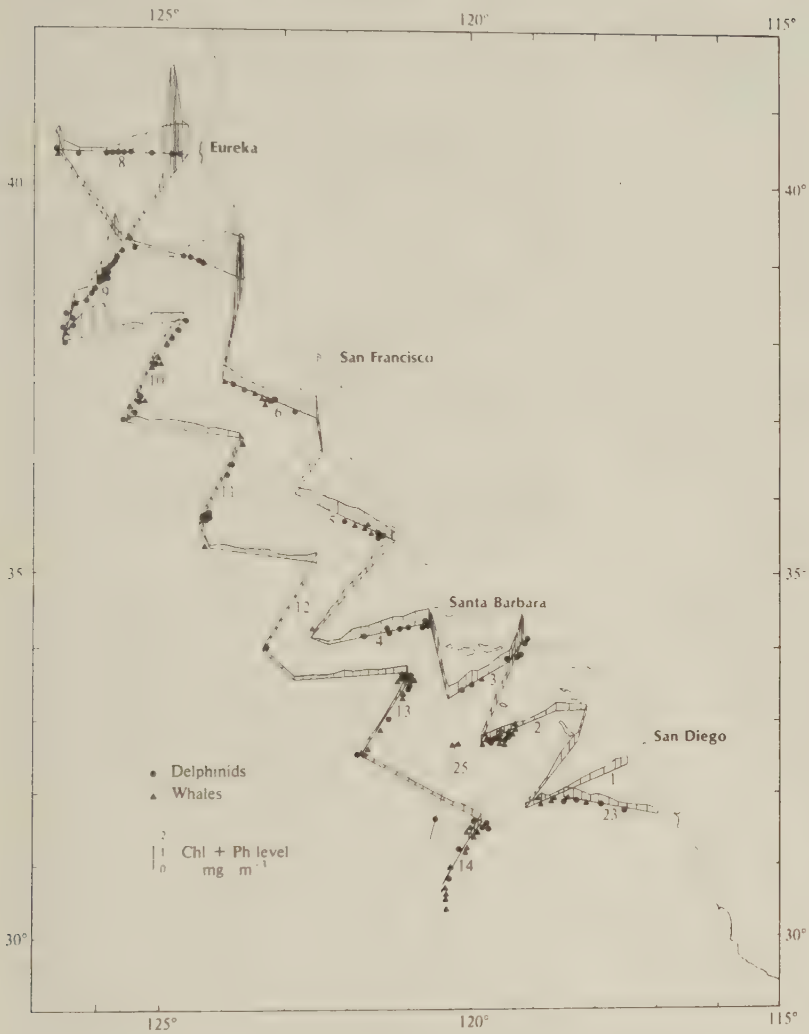

Fig. 1. Northern area of marine mammal survey conducted from the R.V. "David Starr Jordon" between 27 September and 20 October, 1979. Locations of the sighted cetacean schools (delphinids and whales) are indicated by circles and triangles, respectively. The average hourly value of chlorophyll plus pheophytin, in units of mg pigment m^{-3}, is indicated by the along-track histograms. Cruise track is labeled by daily onshore to offshore transects, where "Leg 1" corresponds to 27 September or Julian Day 270. No sightings were made during the "night-time legs" of the cruise

processing and analysis were carried out by means of atmospheric correction and a chlorophyll algorithm (Smith and Wilson, 1980; Gordon and Clark, 1981; Gordon *et al.*, 1983) using software of the RSMAS group at the University of Miami. Statistical analysis of the images was carried out at the UCMBO computer and image processing facility at Santa Barbara. Contemporaneous sea-truth data from the along-track record were used to check the validity of values obtained from the processed satellite images.

The examination of relative abundance of each cetacean species in different parts of the coastal habitat was of primary interest in our work. However, data on relative species-abundance collected from ships are potentially biased, because small schools cannot be seen as far off as can larger schools, and each species has its different characteristic school size and behavior. A correction index was devised to adjust for this undersampling effect among species with small average school sizes (*Phocoenoides dalli*, *Grampus griseus*, *Tursiops truncatus* and *Globicephala* sp.). Adjusted relative abundance was calculated by first taking the mean perpendicular distance from the trackline of the sightings of a given species and dividing by the same for *Delphinus delphis*. The latter is a conspicuous species against which we reference the others. This ratio is a relative sightability correction term which was next divided into the numbers of sightings of the species of interest to obtain an adjusted school abundance. For each species, an adjusted measure of total individuals was then calculated by multiplying the adjusted school abundance by the geometric mean school size (Table 3). The mean perpendicular distance of sightings is widely used to correct for differential sightability, although strictly speaking it is correct only if each species has a negative exponential detection function (Gates *et al.*, 1968; Burnham *et al.*, 1980). Our data were insufficient for rigorous testing of this assumption. The geometric mean school size was used be-

Table 1. Cetacean species sighted in California Current region, between Cape Mendocino and tip of Baja California, during the R. V. "David Starr Jordon" cruise between 27 September and 20 October 1979. The key numbers are used in following tables

Key No.	Specific name	Common name
Dolphins		
1	*Delphinus delphis*	Common dolphin
2	*Phocoenoides dalli*	Dall's porpoise
3	*Grampus griseus*	Grampus
4	*Tursiops truncatus*	Bottle-nosed dolphin
5	*Globicephala* sp.	Pilot whale
6	*Lagenorhynchus obliquidens*	White-sided dolphin
7	*Lissodelphis borealis*	Northern right-whale dolphin
8	*Stenella coeruleoalba*	Striped dolphin
9	*Orsinus orca*	Killer whale
10	Unidentified delphinid	Dolphins and porpoises
Whales/pinnipeds		
1	*Balaenoptera musculus*	Blue whale
2	*Balaenoptera physalus*	Fin whale
3	*Balaenoptera edeni*	Bryde's whale
4	*Megaptera novaeangliae*	Humpback whale
5	Unidentified rorqual	Large whales
6	*Berardius bairdii*	Baird's beaked whale
7	*Mesoplodon* sp.	Beaked whale
8	*Ziphius cavirostris*	Goosebeaked whale
9	Unidentified ziphiid	Beaked whale
10	*Physeter macrocephalus*	Sperm whale
11	*Kogia* sp.	Pygmy or dwarf sperm-whale
12	Other unidentified whale	Whales
13	Pinnipeds	Seals, sea lions

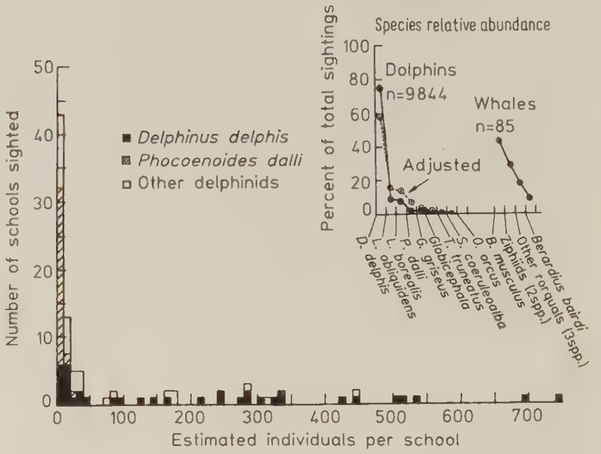

Fig. 2. Number of cetacean schools sighted versus estimated individuals per school. Inset shows species relative abundance. Full specific names are given in Table 1

cause it provides a heavier proportional weighting of the presumed undersampled, smaller school sizes. Since school size may be log-normally distributed for reasons given by Williams (1964) and May (1975), the geometric mean should estimate the median, or most typical, value of actual school size.

Twenty identified cetacean species were encountered during the cruises (Table 1). Fig. 1 shows the locations of the sighted schools from the first cruise off southern and central California; the average hourly value of chlorophyll plus pheophytin is indicated by the along-track histograms.

Results

Cetacean population distributions

Cetaceans were most frequent off the California (USA) coast. On the first cruise 87% and on the second cruise 79% of the schools encountered were north of 30.5° North. The most frequently seen delphinid off California was *Delphinus delphis* or common dolphin (38% of all delphinid schools, Table 2) followed by *Phocoenoides dalli* or Dall's porpoise (25%). The latter, however, was a comparatively rare species in terms of total abundance because its average school size was only 5.7 individuals (Table 2). Most schools among species were small (Fig. 2). Even among *D. delphis,* which had a mean school size of 200 individuals, schools smaller than 20 were seen more often than any other size interval. Since sighting conditions during the second cruise were obtained under relatively adverse weather conditions compared to the first cruise, these and the following statistics are based only upon results north of 30.5° North from the first cruise.

The adjusted species indexes of total individuals (Table 3) show that the dominant delphinid was *Delphinus delphis* (57%), followed by *Lagenorhynchus obliquidens* or Pacific white-sided dolphin (16%), and *Lissodelphis borealis* or northern right-whale dolphin (14%), all being species with relatively large average school size. The remaining species, including *Phocoenoides dalli,* were relatively rare. These latter species are those that were adjusted for differential sightability. The numerical dominance by *D. delphis* is evident, regardless of whether adjusted or nonadjusted measures are used (Fig. 2).

Among the whales, *Balaenoptera musculus,* the blue whale, was the dominant species with 20 schools and 40 individuals (Table 2, Fig. 2). Next were the ziphiid whales, with 18 schools and 43 individuals (among these were *Berardius bairdii, Mesoplodon* sp. and *Ziphius cavirostris*). The remaining 14 rorqual sightings, including *Balaenoptera physalus, B. edeni* and *Megaptera novaeangliae,* constituted the least abundant grouping. *Physeter macrocephalus,* the sperm whale, with 2 schools and 25 individuals, and *Kogia* sp. (probably the pigmy sperm-whale, *K. breviceps*), with 4 schools and 6 individuals, were two species encountered only on the outer legs.

Fig. 1 summarizes the first-cruise locations of sighted cetacean schools; the average hourly values of along-track chlorophyll plus pheophytin (mg pigment m^{-3}) were only obtained during daylight hours, so that only the numbered

Table 2. Numbers of cetacean schools sighted from R.V. "David Starr Jordon", September–October 1979. Key to species names is in Table 1. Dash indicates no sighting made

Julian Day	Leg	Beaufort sea state	Miles searched	Dolphin species										Whale and pinniped species:												
				1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11	12	13
270	1	3–4	88	–	–	–	–	–	–	–	–	–	–	2	–	–	–	1	–	–	–	–	–	–	1	–
271	2	2–3	98	2	–	–	1	–	1	–	–	–	–	4	3	–	–	3	–	–	–	–	–	–	2	7
272	3	2–3	68	3	–	1	2	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	10
273	4	1–4	97	1	1	4	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	11
274	5	2–3	92	1	1	1	–	–	1	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	1	5
275	6	2–3	73	–	–	1	–	–	1	2	–	–	–	4	–	–	1	–	1	–	–	–	–	–	–	1
276	7	1–2	66	1	4	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6
277	8	2–3	96	1	9	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
278	9	1–2	88	10	10	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	7
279	10	1–2	94	2	4	–	–	–	–	1	–	–	2	–	–	–	–	–	–	2	–	1	–	–	2	6
280	11	2–4	94	3	–	–	1	1	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	1	1
281	12	3–4	110	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
282	13	1–2	94	6	–	1	–	–	–	–	1	–	1	3	–	–	–	–	–	–	2	1	–	–	–	9
283	14	1–2	86	3	–	–	–	1	–	–	–	–	2	–	–	–	–	–	–	4	1	–	–	4	2	4
284	15	3–5	101	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
285	16	4–5	109	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
286	17	4	122	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
287	18	4–5	115	1	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–
288	19	3–5	93	1	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–
289	20	5–6	105	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
290	21	3–5	86	2	–	–	–	–	4	–	–	–	1	–	–	1	2	–	–	–	–	–	–	–	1	9
291	22	3–4	115	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
292	23	3	74	4	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–
296	25	2–3	92	–	–	–	–	–	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–
Total schools			2 256	43	29	8	6	4	7	5	1	1	10	20	3	2	3	6	2	6	7	3	2	4	10	76
Mean no. of individuals/school				200.4	5.7	21.3	17.2	23.2	150.3	165.0	3.0	2.0	4.8	2.0	2.0	2.0	1.7	1.3	4.0	2.5	2.0	2.0	12.5	1.5	1.3	5.4
No. of schools/100 miles searched				1.6	1.3	0.3	0.3	0.1	0.3	0.2	>0.0	>0.0	0.4	0.9	0.1	0.1	0.1	0.3	0.3	0.1	0.3	0.1	>0.0	0.2	0.4	3.4
No. of individuals/100 miles searched				335.8	7.3	5.7	4.6	3.1	46.6	36.6	0.1	0.1	2.1	1.8	0.3	0.2	0.2	0.4	0.4	0.7	0.6	0.3	0.5	0.3	0.4	18.2
Temperature (°C)				17.48	15.81	17.48	19.07	20.48	17.83	17.14	19.39	–	18.93	18.75	20.28	23.91	17.13	19.64	16.95	19.59	20.54	19.34	19.28	19.79	–	17.81
Salinity (%)				33.42	33.13	33.52	33.48	33.68	33.60	33.25	33.44	–	33.54	33.58	33.65	33.91	33.70	33.53	33.08	33.45	33.64	33.50	33.03	33.48	–	33.47
Pigment (mg chlorophyll m^{-3})				0.52	1.18	0.73	0.71	0.83	1.22	0.43	0.18	–	0.68	0.58	0.49	0.58	2.0	0.43	0.60	0.22	0.43	0.68	0.12	0.22	–	0.78

Table 3. School size and relative abundance of cetacean species off California, September-October 1979. Table entries listed in order from the largest number of total individuals sighted to the smallest number. Data is a subset from Table 2 and is based upon Legs 1–14, 23, and 25 off southern and central California (Fig. 1). "School size" gives arithmetic means ($\bar{x}_A$), logarithmic means ($\bar{x}_L$), standard deviations (std_L) and geometric mean. "Perp. dist." gives perpendicular distance in nautical miles, based upon sightability characteristics of each species and weightings factors. All delphinids except *P. dalli*, *Grampus griscus*, *Globicephala* sp. and *T. truncatus* are given the same weighting factor (wt = 1); of the latter group, *Globicepha* sp. and *T. truncatus* are given equivalent weights. The weighting factor for a given species is the mean perpendicular distance, $\bar{d}$, divided by the same for *D. delphis* ($\bar{d}$ = 1.759). "Tot. individs" gives adjusted index of total individuals = (*n*)(geometric mean) ÷ (wt); whales were not adjusted, as school and sample sizes were small

Species	Sightings (n)	School size				Perp. dist. (nm)		Tot. individs	
		$\bar{x}_A$	$\bar{x}_L$	std_L	Geom. mean	$\bar{d}$	wt	non-adj. (arith.)	adj. (geom.)
Dolphins									
Delphinus delphis	38	201.0	1.89	0.745	77.6	1.759	1.00	7 639	2 950
Lagenorhynchus obliquidens	3	298.3	2.44	0.213	275.4	1.759	1.00	895	826
Lissodelphis borealis	5	165.0	2.15	0.265	141.3	1.759	1.00	825	706
Phocoenoides dalli	29	5.7	0.64	0.325	4.36	0.617	0.35	165	361
Grampus griseus	8	21.3	1.17	0.433	14.8	1.336	0.76	170	156
Globicephala sp.	3	30.0	1.44	0.231	27.5	1.348	0.77	90	107
Tursiops truncatus	4	13.8	0.94	0.489	8.7	1.348	0.77	55	45
Stenella coeruleoalba	1	3.0	0.48	–	3.02	1.759	1.00	3	3
Orsinus orca	1	2.0	0.30	–	1.99	1.759	1.00	2	2
Whales									
Balaenoptera musculus	19	1.95	–	–	–	–	–	37	–
Other rorquals	10	1.50	–	–	–	–	–	15	–
Ziphids except *Berardius bairdii*	12	2.08	–	–	–	–	–	25	–
Berardius bairdii	2	4.00	–	–	–	–	–	26	–
Physeter macrocephalus	3	8.67	–	–	–	–	–	26	–
Kogia sp.	4	1.50	–	–	–	–	–	6	–

daytime legs of the cruise have sightings indicated, whereas chlorophyll measurements were made both day and night. Many of the sightings or groups of sightings (Fig. 1) were in the vicinity of seafloor topographical changes and regions of relatively persistent, high chlorophyll. For instance, the sightings at the ends of Legs 1 and 2 were in the vicinity of the Tanner and Cortez Banks, an area important to fishermen. On Leg 5, the whale sightings occurred near Pioneer Seamount, an area that once supported a nearshore whaling industry (Rice, 1963 b). Sightings along Leg 8 occurred along the topographically complex Mendocino Escarpment. Thus, casual observation would suggest that cetacean schools are concentrated in waters of relatively rich productivity and are not distributed at random among different chlorophyll concentrations.

There is, however, a stochastic element to the shipboard observations, which might explain the above. To test whether cetaceans have a random distribution with respect to chlorophyll in space, all sightings were divided into several chlorophyll concentration intervals. The sightings within chlorophyll concentration intervals were then averaged or normalized by the different number of daylight transect blocks within each concentration interval. Transect blocks are one-minute time intervals of integrated along-track chlorophyll data (including time intervals without cetaceans), each corresponding to a distance of roughly 300 m (at 10 knots). The chlorophyll value used to represent a sighting was the mean of 25 transect blocks, equal to ± 12 min from the actual point of sighting to account for a "nominal sighting radius", which provided values of an average and a variance (see below) of chlorophyll for the vicinity of the sighting location. Fig. 3, using all marine mammal sightings, shows the number of (a) sightings versus chlorophyll concentration in five intervals ($0.01 < 0.03$, $0.03 < 0.1$, $0.1 < 0.3$, $0.3 < 1.0$, $1.0 < 10$) in units of mg pigment m^{-3}, (b) daylight transect blocks for each of these same five chlorophyll intervals, and (c) the corresponding number of sightings normalized by the number of daylight transect blocks.

Also shown in Fig. 3 a, by the dashed histogram values, are the number of sightings that would be expected in each chlorophyll interval if the mammals had been randomly distributed with respect to chlorophyll concentration and would thus have been sighted in proportion to the distance searched (i.e., in proportion to the number of daylight transect blocks in each chlorophyll interval as shown in Fig. 3 b). A chi-square test of the hypothesis that the cetaceans were sighted in proportion to the number of daylight transect blocks in each range led to rejection of the hypothesis of a random distribution of sightings with respect to chlorophyll concentrations at the 99% confidence level (DF = 4, $\chi^2 = 33.6$). The number of sightings per daytime transect block was also regressed against the mean chlorophyll concentration of each interval (Fig. 3 c) and gave a sample correlation coefficient of 0.92. A Student's *t*-test indicated that the slope of this regression was significantly different than a slope of zero (DF = 3, $0.05 > P > 0.01$), providing further evidence for rejection of

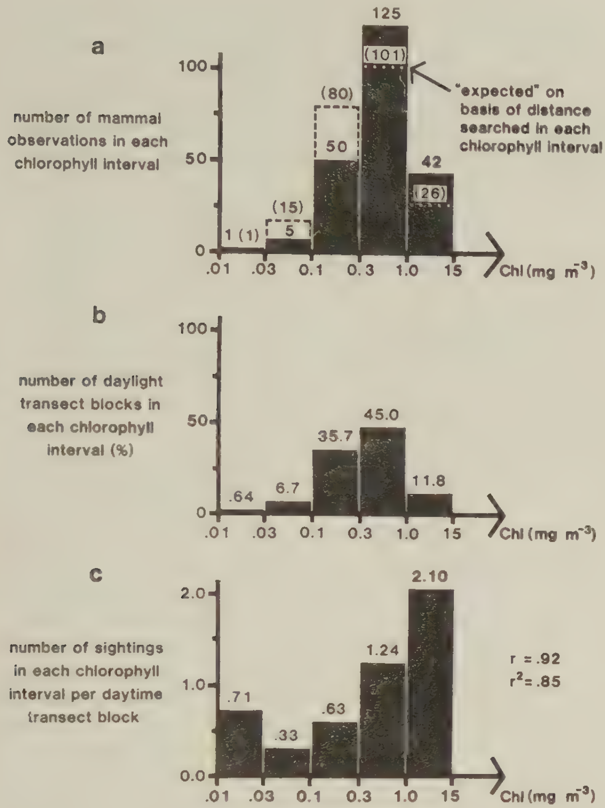

Fig. 3. (a) Number of marine mammal sightings versus chlorophyll concentration divided into five logarithmic intervals ($0.01<0.03$, $0.03<0.1$, $0.1<0.3$, $0.3<1.0$, $1.0<10$, in units of mg pigment m^{-3}); dashed "expected" lines show number of observations based on assumption of a random distribution in proportion to number of daytime transect blocks searched in each interval of chlorophyll concentration. (b) Number of daylight transect blocks (%) in each chlorophyll interval for all mammal sightings; transect blocks are one-minute intervals of shipboard observations. (c) Number of sightings per daytime transect block (arbitrary normalization) versus chlorophyll concentration ($n=223$, $r=0.92$)

the hypothesis of no dependence. This also provides a measure of the degree of correlation between sightings per daytime transect block and chlorophyll concentration, and is consistent with the hypothesis that more sightings occur at higher chlorophyll concentrations.

The robustness of these statistics was tested by distributing the data into several different numbers of equally spaced (on a log scale in order to span three orders of magnitude in chlorophyll concentrations) chlorophyll intervals and also by selecting the chlorophyll intervals with the requirement of obtaining an equal number of transect blocks per chlorophyll interval, again for several different numbers of intervals. In all these cases, chi-square tests of the data and *t*-tests of the corresponding regression slopes against zero lead to rejection of the hypothesis that the marine mammal sightings were independent of chlorophyll concentration.

Sightings of individual species were too few, once they were divided into appropriate chlorophyll concentration intervals, to allow for meaningful statistical testing of their distributions in space. However, separate tests were done for the combined mysticeti or baleen whales and for the combined odontoceti or toothed whales. There were only 30 observations of the former, and a chi-square test of the hypothesis that they were distributed randomly with respect to the chlorophyll concentration gave a value just below the 90% level of confidence (DF=4, $\chi^2=7.3$). Also, a *t*-test of the slope of this regression indicated that it was not significantly different from zero (DF=3, $P>0.10$). Thus, at this level of confidence, one could not decisively reject the hypothesis that mysticeti were distributed randomly with respect to chlorophyll concentration. In contrast, a chi-square test of the odontocete sightings led to a rejection of the hypothesis of a random distribution at greater than the 97.5% confidence level (DF=4, $\chi^2=12.6$). The number of sightings of odontocetes per daytime transect block was also regressed against chlorophyll concentration, giving a sample correlation coefficient of 0.81. A *t*-test of the slope of this regression against zero showed it to be in a borderline area between significance and nonsignificance (DF=3, $0.10>P>0.05$). These results are consistent with the hypothesis that toothed whales are found more frequently at higher chlorophyll concentrations.

Cetaceans and chlorophyll variance

Shipboard observations of along-track chlorophyll concentration and marine mammal schools suggested that some species were not only associated with regions rich in chlorophyll but also with areas where major changes in the surface characteristics occurred, e.g. at interfaces such as drift lines, shear zones, convergences and the coastal-offshore water boundary.

Our along-track data provided a measure not only of the concentration of chlorophyll but also of its variance. Continuously recorded along-track data can, for convenience of analysis, be integrated into 1-min intervals which we refer to as transect blocks. Any number of these transect blocks can be further averaged to obtain a mean and standard deviation of the along-track data for some distance in a given time interval over which the ship has traveled. The mean and standard deviation of all pigment recorded ± 12 min of each sighting was calculated. Twenty-five min is approximately equal to 4 nautical miles of track data and is equivalent to 7 km or 5 satellite pixels (picture elements) at a speed of 10 knots. This provided a "nominal sighting radius" of a circle encompassing the sighted mammals. The radius was chosen small enough so that chlorophyll variance would be sensitive to sharp frontal boundaries yet large enough so that mean chlorophyll would be representative of the region around the sighting. A doubling or halving of the chosen radius did not significantly influence the statistical results. Thus, for each sighting location an average and a coefficient of variation of the

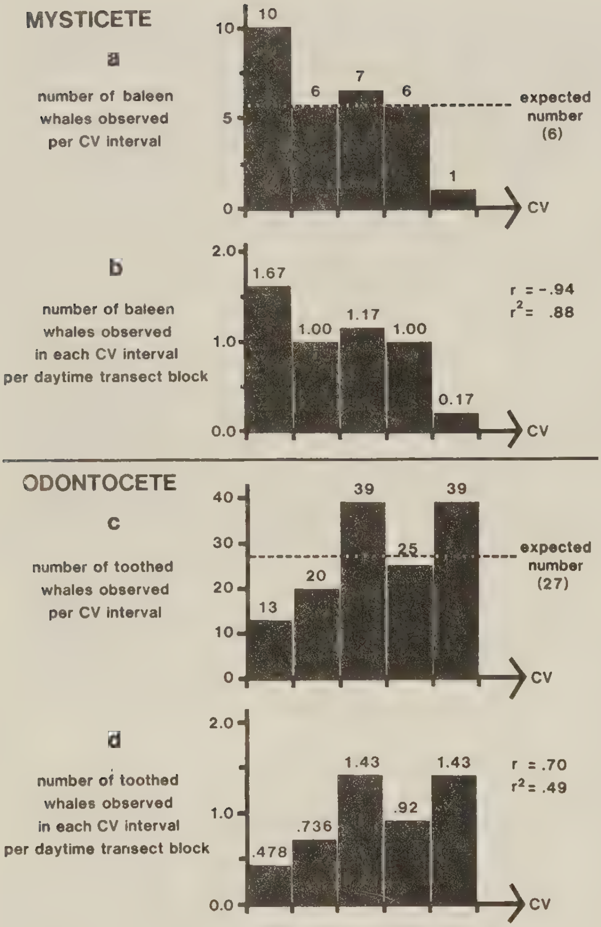

Fig. 4. Number of mysticete (baleen) whale sightings (a) and number of odontocete (toothed) whale sightings (c) versus chlorophyll coefficient of variation (CV) divided into equal frequency intervals. Expected number of observations based on assumption of a random distribution with respect to CV is shown by dashed line. (b) and (d) Number of mysticete ($N=30$, $r=-0.94$) and odontocete ($N=136$, $r=0.70$) whale sightings per daytime transect-block

along-track pigment concentration within this "nominal radius" was calculated. These calculations are both meaningful for sighting statistics and useful in providing a means whereby both ship and satellite data can be directly intercompared (see "Discussion").

We compared the number of schools of Mysticeti and of Odontoceti at five different levels of coefficient of variation (CV) of chlorophyll concentration. The CV will be relatively large in regions of high chlorophyll variability, such as frontal regions, and relatively small in areas where the chlorophyll concentration is homogeneous. Fig. 4 a and b show the data for mysticete whales; Fig. 4a the number of these whales observed as a function of the CV of chlorophyll concentration, Fig. 4 b the number observed per daytime transect block with respect to CV. Fig. 4 c and d show similar data for odontocetes. The CV was subdivided into intervals such that there were an equal number of transect blocks per CV interval, so that if the observations were randomly distributed in space, one would expect an equal number per CV interval. This "expected" number of sightings per CV interval is indicated on Fig. 4 a and c by dashed lines.

For mysticete whales, a chi-square test comparing the observed and expected frequency of sightings for each interval gave a chi-square of 7.10 (DF=4, $P=0.14$) so that the hypothesis of a random distribution with respect to chlorophyll variation could not be rejected at the 90% level of confidence. It is still of interest, however, to note that a regression of normalized observations versus CV (Fig. 4 b) gave a correlation coefficient of $r=-0.94$. A t-test of the slope of this regression with that of zero indicated that it is significantly different from zero (DF=3, $0.05>P$). If this tendency for mysticete observations to be more numerous in areas of low chlorophyll variation were to be confirmed by further research, it would indicate a sharp contrast in this habitat descriptor as compared to that for odontocetes.

For odontocetes, a chi-square test comparing the observations against the hypothesis of an independent distribution with respect to chlorophyll CV indicated that the null hypothesis could be rejected (DF=4, $\chi^2=19.7$, $0.01>P$). In contrast to the baleen whales, the normalized sightings of toothed whales showed a positive correlation ($r=+0.70$) with CV. This suggests that higher numbers of odontocete sightings occurred in regions of relatively high chlorophyll variability.

Cetaceans and physical water types

The above chlorophyll statistics, which may serve as habitat descriptors, are also associated with the conventional physical parameters used to characterize water masses. For example, a major break in surface temperature and salinity often occurred at the coastal-offshore water boundary which also often differentiated regions of low and high chlorophyll concentration (Fig. 5). This boundary tended to correspond to the surface-density isopleth, $\sigma_t=23.8$. Sigma-t is determined from temperature and salinity (see Sverdrup *et al.*, 1942) and, off California, decreases with offshore distance (see Lynn *et al.*, 1982). A classification of the cetacean sighting data as coastal or oceanic, on the basis of interrelationships between temperature, salinity and chlorophyll, and the relationship to fronts, tended to be separable by this sea-surface density interface. Fig. 5 shows that *Delphinus delphis* were encountered in outer coastal and in oceanic waters, while *Phoecoenoides dalli* were encountered primarily in coastal waters, as indicated by the dashed envelope lines relative to the $\sigma_t=23.8$ line.

In the satellite imagery a persistent color/temperature front was also recognizable. Water inshore of this color/temperature front (high density, salinity and chlorophyll but low temperature) had characteristics of recently upwelled water. The water offshore this front was characteristic of subarctic water of the California Current system (Hickey, 1979). This break between oceanic and coastal waters was often accompanied by abrupt changes in the encounter rate of birds and mammals. We have therefore used this color/temperature front as the seaward boundary of coastal water. This front is shown in two satellite chlorophyll images in Figs. 6 a and 7. It persisted more or less coincident with the slope break (2 000 m isobath) for the entire period of the cruise.

The ship sampling-intensity by itself was not adequate to give a detailed areal picture of the complexity of the coastal-oceanic boundary. However, mesoscale features were indicated by abrupt changes in the along-track data. From the satellite data, these mesoscale features can be identified (Fig. 6 a). Comparison of the ship and satellite data showed that strong fronts were most apparent in the along-track data where the ship entered or left these mesoscale features and crossed one water type, or habitat, to another.

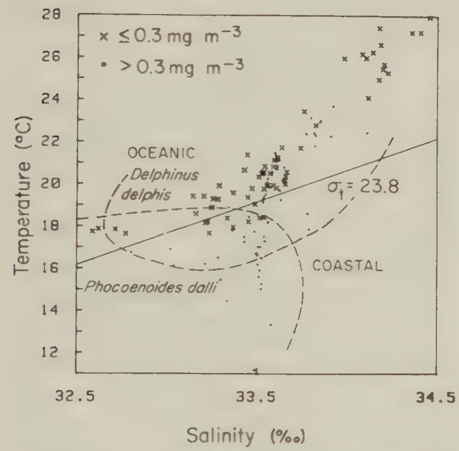

Fig. 5. Temperature–salinity diagram for surface waters in surveyed area. Sightings from areas with greater than 0.3 mg pigment m^{-3} are indicated by dots, those from areas with less than 0.3 mg pigment m^{-3} by crosses. Diagram shows relationships between the color/temperature front, the physical properties of the water masses, and cetaceans. *Delphinus delphis* were encountered in outer coastal and in oceanic waters, while *Phocoenoides dalli* were encountered primarily in coastal waters, as indicated by the dashed envelope lines relative to the $\sigma_T = 23.8$ line

The field investigation sampled relatively less of the offshore oceanic water, so there are fewer data concerning the importance of that province as a cetacean habitat. If the coastal water were the major habitat, there would be greater numbers and more species seen in coastal versus oceanic water, relative to the allocation of sampling effort in the two kinds of water. This follows because, as discussed above, most cetaceans were found in higher chlorophyll waters which, in these areas and at this time, were usually coastal waters. Cetacean schools were indeed more frequently encountered in coastal waters than expected on the basis of sampling effort, but the statistical significance of this difference varied according to the stratification of the sample, as shown by several chi-square tests (Table 4). Significantly more cetaceans were sighted in coastal waters than oceanic waters ($P<0.01$) when all schools of cetaceans species were combined, either over the entire area or only off central California. Water types within the Southern California Bight are more complex and do not lend themselves as readily to simple water-mass description; here, the distributions with respect to water masses becomes problematical. Delphinid cetaceans by themselves were significantly more frequent in coastal waters over the entire area and in the Southern California Bight, but not off Central California. In general, a finer stratification of our data led to fewer observations and less significant statistical results.

Individual species and habitat descriptors

Because the relationship between along-track pigment levels to cetacean sighting are significant for the combined populations, it is instructive, in spite of the potential limitations of finer stratification, to consider if water types and/or chlorophyll concentrations may characterize habitat differences among individual cetacean species. To in-

Table 4. Cetacean distribution by water type Water type was determined by inspection of along-track records of temperature and salinity; chi-square tests were based upon miles sampled in the two kinds of water. Miles searched were along Legs 1–14, 23 and 25

Area	Miles searched			Schools observed											
				All cetaceans				Dolphins only[a]				Whales only			
	Coastal	Oceanic	Total	Coastal	Oceanic	Total	χ^2	Coastal	Oceanic	Total	χ^2	Coastal	Oceanic	Total	χ^2
Southern California Bight	118.6	389.5	508.1	18	32	50	3.799	9	11	20	4.098*	9	21	30	0.419
Central California	659.6	243.6	903.2	82	17	99	4.341*	61	13	74	2.863	21	4	25	1.019
Pooled	778.2	633.1	1 411.3	100	49	149	8.158**	70	24	94	13.43**	30	25	55	1.316

[a] Family Delphinidae * $P<0.05$ ** $P<0.01$

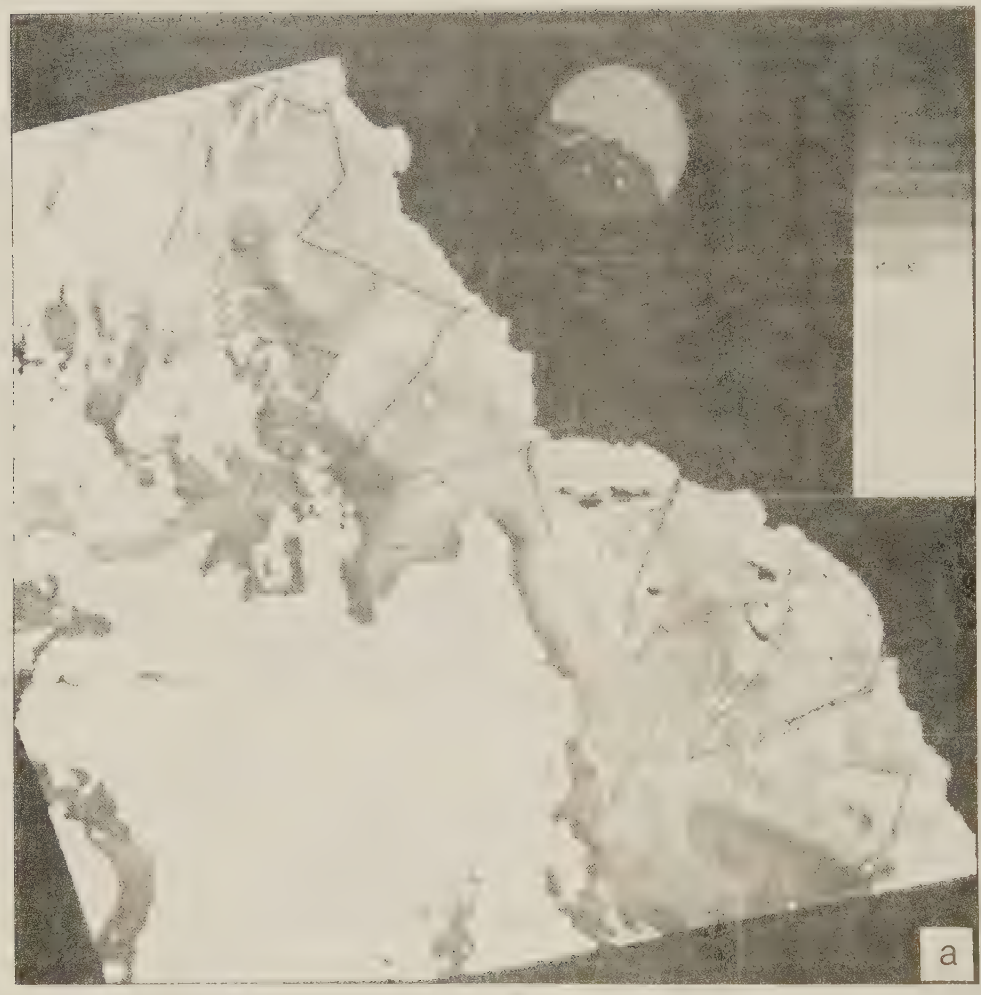

Fig. 6. (a) Processed Coastal Zone Color Scanner image of the California coastal region. Orbit 4749, 2 October 1979; image consists of 512 × 512 pixels, where one pixel (i.e., one picture element) represents a surface area of roughly 1.5 × 1.5 km. Phytoplankton pigment concentration (chlorophyll plus pheophytin) ranging from 0.01 to 10 mg pigment m^{-3} is represented by 18 equally-spaced logarithmic steps from low (dark) to high (light) concentration; black areas are land or clouds masked during processing; each leg of cruise track is superimposed on the image and numbered; Leg 1 corresponds to Julian Day 270. Image was obtained during approximately 4-min period near noon on 2 October 1979 (Leg 6, Julian Day 275) while R.V. "David Starr Jordan" was off Monterey Bay (Fig. 1). (b) Variance of chlorophyll image of surveyed area. Orbit 4749, 2 October 1979 (Julian Day 275)

vestigate this hypothesis, we calculated several pigment concentration statistics for each species analogous to those discussed above. First was the pigment concentration measured at the location of the species sighting. Because of small-scale variations in pigment concentrations (Platt and Denman, 1980; Smith and Baker, 1982) we also used the values of pigment recorded ± 12 min of each sighting to obtain the pigment mean as well as the pigment variance within a small distance of the sighting. Second, we determined from the ± 12 min of pigment measurements the "within" sighting variance (Sp^2), and the "between" sighting variance (Sm^2) from all combined sightings of each species. That is, we decomposed the total pigment variance of each species into a portion due to variation within the sighting area and into another portion due to variation between the sightings (Dixon and Massey, 1969; Sokal and Rohlf, 1969). Finally, we recorded the minimum and maximum range of pigment concentrations within which each species was sighted (Table 5). Our objective was to document not only the mean and variance of the chlorophyll within a habitat, but also to investigate whether selected species were sighted from a relatively homogeneous population of chlorophyll concentrations or from areas of widely differing chlorophyll concentrations.

Recognizing that an adequate sample size did not exist for all species sighted, a subset of species was used to test

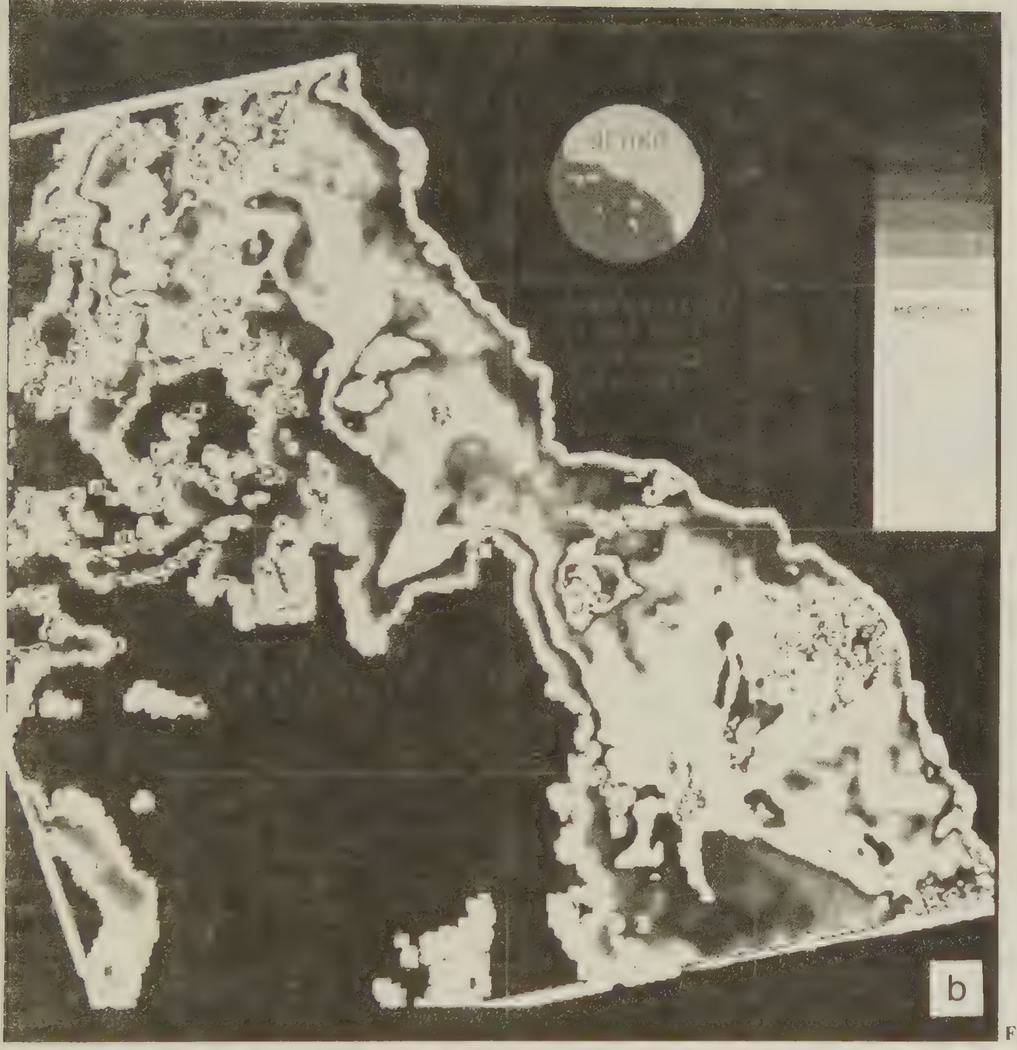

Fig. 6. (continued)

Table 5. Characterization of marine mammal habitats by pigment (chlorophyll) concentration. BCV: between-sighting coefficient of variation; WCV: within-sighting coefficient of variation

Species	Ship data					Satellite data				
	Sightings (*n*)	Pigment (mg chl m^{-3})		BCV	WCV	Sightings (*n*)	Pigment (mg chl m^{-3})			
		Range	$\bar{x} \pm Sm$	$Sm/\bar{x}$ (%)	$Sp/\bar{x}$ (%)		Single pixel		Sighting area	
							$\bar{x} \pm \sigma$	CV	$\bar{x} \pm \sigma$	CV
1 *Delphinus delphis*	38	0.014–2.40	0.36 ± 0.40	112	27	9	0.64 ± 0.52	81	0.57 ± 0.29	50
2 *Phocoenoides dalli*	29	0.13–2.80	0.89 ± 0.76	86	28	1	0.50		0.60	
3 *Grampus griseus*	8	0.61–0.83	0.71 ± 0.09	13	11	3	1.21 ± 1.12	93	0.77 ± 0.36	47
4 *Tursiops truncatus*	6	0.12–1.81	0.45 ± 0.47	104	60	1	0.35		0.36	
6 *Lagenorhynchus obliquidens*	7	0.43–2.49	0.92 ± 0.62	68	25	2	0.42 ± 0.04	9	0.51 ± 0.05	9
1 *Balaenoptera musculus*	16	0.16–0.96	0.45 ± 0.26	59	10	14	0.38 ± 0.22	58	0.47 ± 0.17	37
5 Unidentified rorqual	6	0.12–0.86	0.31 ± 0.28	92	13	6	0.83 ± 1.28	154	0.40–0.32	80
8 *Ziphius cavirostris*	7	0.12–0.97	0.31 ± 0.24	79	52	4	0.50 ± 0.19	38	0.60 ± 0.31	52
10 *Physeter macrocephalus*	2	0.12–0.33	0.17 ± 0.09	54		2	0.18 ± 0.04	21	0.16 ± 0.04	25
13 Pinnipeds	56	0.08–1.87	0.60 ± 0.49	82	24	16	0.63 ± 0.46	73	0.55 ± 0.23	42

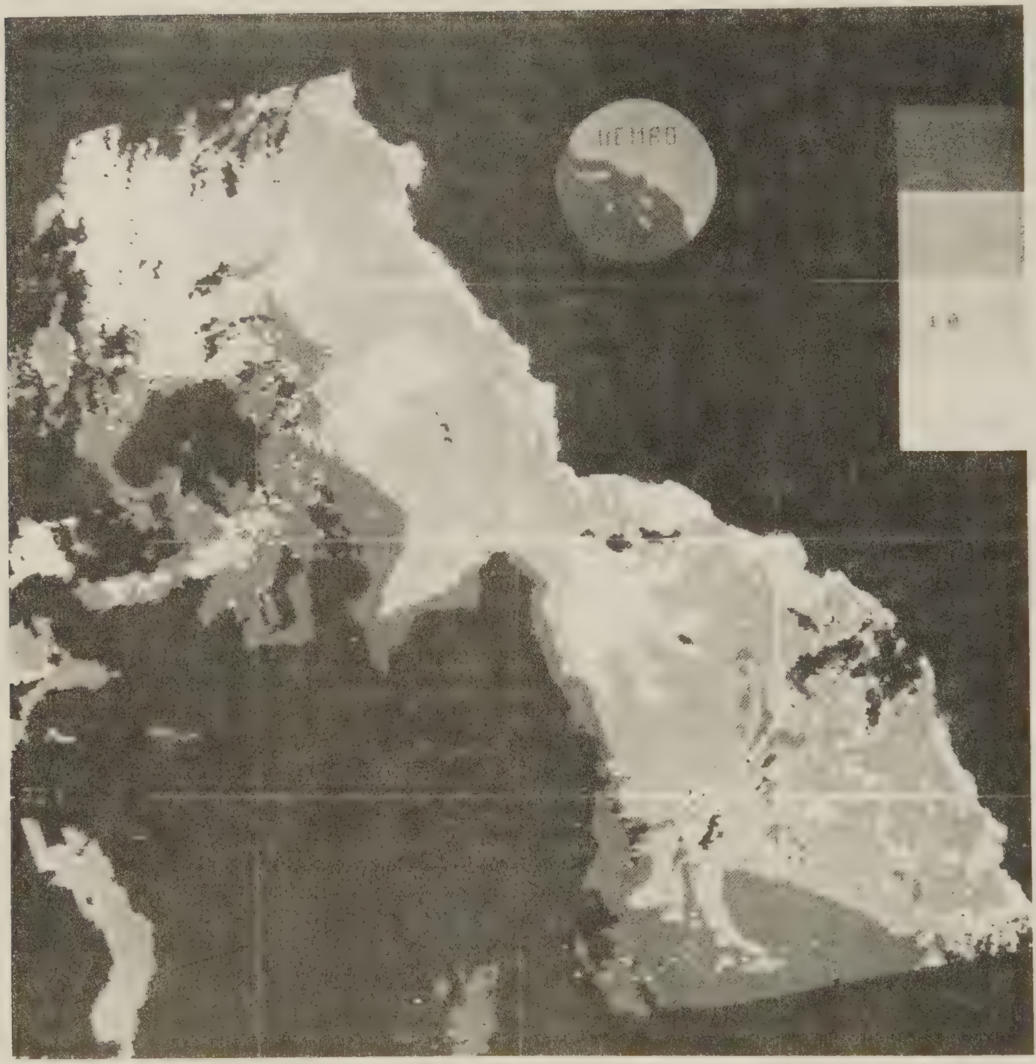

Fig. 7. CZCS image of California coastal region. Orbit 4749, 2 October 1979 (Julian Day 275) processed to show low (<0.3 mg pigment m^{-3}), medium (0.3 to 1.0 mg pigment m^{-3}) and high (>1.0 mg pigment m^{-3}) chlorophyll habitats

whether the sightings for a given species demonstrated statistically significant fidelity to a specific range of chlorophyll concentrations. An analysis of variance *F*-test was used to determine if the average chlorophyll variance from a set of species sightings was significantly larger than the variance of the sighting means. The between and within CVs of pigment level from the ship data are given in Table 5 for each of these species. The between-sighting coefficient of variation, given in Table 5, provides an index of the pigment habitat variability from one sighting to the next for each species (Sm^2). The within-sighting coefficient of variation provides a measure of the pooled variance for all sightings (Sp^2). If the sightings are from populations having unequal means, then (Sm^2) will be considerably larger than (Sp^2). For each species, except *Grampus griseus*, we could reject the hypothesis by *F*-test that its sightings were from areas with the same mean chlorophyll level, i.e., within the chlorophyll range for a species, fidelity to a specific chlorophyll habitat was low.

Estimates of within-habitat heterogeneity (CV of the mean variance of the chlorophyll concentration) showed there were differences between species not correlated with absolute pigment levels. For example, *Delphinus delphis* was widely distributed in heterogeneous, medium-chlorophyll environments, while *Balaenoptera musculus* was sighted predominately in less variable, medium-chlorophyll regions. *Phocoenoides dalli* and *Lagenorhynchus obliquidens* were sighted primarily in medium-to-high chlorophyll waters, whose means exhibited significant chlorophyll differences at each sighting (chlorophyll concentrations ranged from 0.13 to 2.8 and 0.4 to 2.5 mg pigment m^{-3}, respectively; Table 5).

In contrast, pigment differences between *Grampus griseus* sightings suggest that this mammal is attracted to much more constant environments (0.61 to 0.83 mg pigment m^{-3}). Comparison of its between and within sighting CVs supports the hypothesis ($0.05 > P$) that the sightings were in waters with the same mean chlorophyll concentration. However, this result is primarily suggestive since the number of sightings is few.

Interestingly, the more geographically restricted *Phocoenoides dalli* commonly occurred over a wider range of absolute chlorophyll levels within the generally high chlorophyll areas off northern central California than did the widespread *Delphinus delphis,* which tended to occur in offshore waters. Evidently the more productive habitat of *P. dalli* is also characterized by large and changing variations in pigment level. Also, the data suggest that *Lagenorhynchus obliquidens* and *Lissodelphis borealis* are primarily coastal water species. On the other hand, *Physeter macrocephalus* (Rico, 1977) and *Kogia* sp. are clearly oceanic by geography and water type. Other species, especially ones occurring in or near the Southern California Bight (an area of much water-mass mixing), occurred in both kinds of water.

Satellite images

Both qualitative experience and our statistics suggest that oceanic chlorophyll concentrations and sea-surface temperatures, as well as the variance of these properties, can be used as "habitat descriptors" for living marine resources. As a working hypothesis, it could be assumed that habitats of some Cetacea are primarily defined by areas with relatively high chlorophyll concentrations. In California waters at this time of year these are primarily defined by the coastal, high-chlorophyll and low-temperature surface waters. It follows that the mesoscale dynamics of these waters, especially those determining distribution and relative productivity, are important to the different species of Cetacea. Our results indicate that this hypothesis holds when all observations are aggregated; however it is quite likely that this habitat-descriptor hypothesis will also hold at some level of generality for some individual species. We would also emphasize that the data necessary to adequately test, and to optimally use, this hypothesis have not yet been collected.

Table 5 also shows the characterization of marine mammal habitats by pigment concentration as derived from satellite (CZCS) imagery. The table lists sightings for which contemporaneous satellite imagery was available ±6 h of a shipboard sighting. The mean pigment concentration from the satellite picture elements ("sigle pixel") corresponding to the sighting locations are given, along with the standard deviation and coefficient of variation of this pigment concentration from the average of all sighting locations. The "sighting area" data were obtained by first averaging all the pixels within a 7 km × 7 km (5 × 5 pixel) box centered on the sighting location, and then taking a mean of all these data. This area on the satellite image is approximately the area within the "nominal sighting radius" discussed above, and therefore provides an analogous mean, standard deviation and coefficient of variation for comparison with the ship data. Although the satellite data are consistent with the ship data, there are fewer sighting statistics because satellite passes and/or cloud-free imagery did not exist at the time of all shipboard sightings.

Fig. 6 a shows a chlorophyll image of the California coastal region during the period of the cruise. The absolute accuracy of this image is estimated to be (by comparison with ship data) ±40%. Our point of departure for the work reported here is the derived chlorophyll image. The black areas of these images are either land or clouds which have been set to zero value. Landmarks (e.g. Point Conception, Santa Barbara, San Diego, the offshore islands) are easily identifiable by comparing Fig. 1 with the images. Phytoplankton pigment concentrations ranging from 0.01 to 10.0 mg pigment m^{-3} are represented by 18 equally-spaced logarithmic steps from low (dark) to high (light) concentration, corresponding to the grey scale on the images. The ship track (annotated for each leg of the cruise) has been superimposed on the image, and also can be compared with Fig. 1. Note that each processed image not only represents a synoptic view of the relative chlorophyll concentrations in the area observed, but also is a matrix of quantitative information: the chlorophyll concentration at each pixel (each "picture element" corresponds to a surface area of roughly 1.5 km × 1.5 km) location. As a consequence, statistical analyses can be carried out using such images (Smith and Baker, 1982; Smith *et al.*, 1982). The variance based on the image displayed in Fig. 6 a is depicted by Fig. 6 b. This "variance image" clearly demonstrates the area of high chlorophyll variability (lighter) and the area of more constant habitats (darker). Note that the offshore oceanic region is represented as a much more constant environment than many inshore coastal regions. Again, the offshore clouds which have been masked black during processing must be disregarded.

Estimates of the distributions and abundances of cetaceans are usually imprecise owing to the methods of surveying their habitats. Airplane searches provide data from low-flying, fast-moving platforms, while ships allow for more careful observations from a slower-moving platform. Both assume that all animals in the path are seen, while realizing that many of them may avoid the ship or may be underwater at the time of the overflight. In addition, it is known that the time that a cetacean spends at the surface is highly variable and somewhat species-specific. Using current techniques, a species abundance may be estimated from counts of schools per unit area adjusted for detectability (Burnham *et al.*, 1980) and then multiplied by mean school size and the total area searched to obtain an esimate of total abundance. Alternatively, if our habitat-descriptor hypothesis holds and if a cetacean species could be associated with a given range of chlorophyll concentration, then the number of individuals per track-line area of the specific habitat searched (to total track-line area searched) could be normalized by the specific habitat area (to total area searched) for the region under study to obtain an estimate of total abundance.

For example, the image in Fig. 6a has been divided into three grey scale levels (Fig. 7) corresponding to low (<0.3 mg pigment m^{-3}), medium (0.3 to 1.0 mg pigment m^{-3}) and high (>1.0 mg pigment m^{-3}) chlorophyll concentrations. These habitat divisions are based on the shipboard data as well as upon the clearly delineated color/temperature front as seen in Fig. 6. An immediate result from this habitat image is a quantitative estimate of the three habitat areas. The non-cloudy area shown in this image is approximately 211 000 km², and the areas of low, medium and high chlorophyll correspond to 79 000, 114 000, and 18 000 km² or 37, 54 and 9% of the total cloudless area, respectively. A second observation from the satellite imagery is that the color/temperature front was relatively persistent (± 10 km of mean position) during the two weeks of the survey in this region off the California coast, indicating that these habitats may be rather persistent.

If shipboard observations can establish characteristics of species habitats, satellite imagery can then be used to estimate habitat areas for calculating species abundances within these areas. For example, *Grampus griseus* was found to be associated with a relatively narrow range of chlorophyll waters (Table 5). If we assume that the habitat for this species is "medium" chlorophyll waters, then its abundance may be more accurately estimated from an expansion of density calculated from the miles searched in that habitat and expanded to the total areal extent of only medium chlorophyll waters. Thus, the total nautical miles (nm) searched within medium chlorophyll waters was 12 465 nm (or 41.3% of the total miles searched). Since the area of this habitat was 54% of the total habitat, we might expect *G. griseus* schools to be 30% ($0.54 \div 0.41$) more abundant than an estimate that assumed the species habitat was the total area.

Other cetaceans seem to be associated with high chlorophyll areas (e.g. *Phoceoenoides dalli* and *Lagenorphynchus obliquidens*). When sightings for these species were superimposed on the satellite imagery, it could be seen that they occurred in near-shore, high-chlorophyll regions or in the high-chlorophyll areas of color fronts. If we were confident of the fidelity of these marine mammals to these habitats, population estimates could be based on the areas of high-chlorophyll water only.

During our survey, *Mesoplodon* sp., *Physeter macrocephalus* and *Kogia* sp. were associated with low-chlorophyll waters on the seaward side of the color/temperature front. This habitat is estimated as 47.5% of the total area, based upon the miles searched in such waters, but only 37% of the area as determined from satellite imagery. We would therefore assume that abundance estimates of these species would be adjusted down by 22% ($1.0-0.37 \div 0.475$).

Discussion

Cetaceans were sighted in coastal water more frequently than expected on the basis of sampling allocation. Our data strongly suggest that in California coastal waters the numerous cetacean sightings were associated with chlorophyll-rich waters which, in turn, are linked to both high primary production (Owen, 1974) and rich and diverse fisheries and ichthyofauna (Horn, 1980). These waters thus appear to be a major habitat of cetaceans. While our work is exploratory, it suggests that more extensive ship/aircraft/satellite stratified sampling will be required for more reliable statistics on cetacean populations. Further, this work indicates that more extensive, quantitative information on ocean water types and possible habitat descriptors should be obtained in conjunction with distribution and abundance surveys. Although the possibility that species aggregate in response to habitat productivity and variability is not the only plausible hypothesis consistent with our observations, the methodology discussed shows the possibility of quantitatively testing this and alternative hypotheses.

Total cetacean sightings per daytime transect block were highly correlated with increasing chlorophyll concentrations ($r=0.92$, Fig. 3c). While a stratification by suborder suggested (the chi-square test was not significant at the 90% level) that mysticete whales are only weakly correlated ($r=0.62$) with surface chlorophyll concentrations, the odontocetes were significantly and positively correlated ($r=0.81$) with chlorophyll concentration. A chi-square test to determine if these whales had a random distribution with respect to chlorophyll allowed rejection of this null hypothesis at the 97.5% confidence level. Although it is clear that a significant correlation exists between cetacean sightings and primary production (as measured by pigment biomass), the degree of "coupling" and the ecological significance of these observations is not obvious. A possible hypothesis is that the distribution and abundance of cetaceans are defined by the coastal surface-water mass, which is rich in chlorophyll, and the link is via the food web. However, these "links" are likely to be species-specific and may be indirect. For example, Evans (1981) suggested that *Delphinus delphis* were concentrated at seamounts and along escarpments, not necessarily because of the high concentrations of chlorophyll there, but because this species was using multisensory environmental cues related to these landmarks to orient during migration.

We have also shown that there is a significant relationship between the sightings of certain cetaceans and the coefficient of variation (CV) of chlorophyll. Further, when stratified to suborder, the toothed whales were significantly correlated with areas of relative high CV, while the baleen whales showed a weak, but non-significant, negative correlation (Fig. 4). The similar results obtained for chlorophyll concentration and CV may be due simply to the fact that chlorophyll is, in many regions, correlated with its own CV.

The cetacean fauna was numerically dominated by *Delphinus delphis* among the delphinid odontocetes and by

Balaenoptera musculus among the whales. *D. delphis* is generally considered the most abundant cetacean off California (Rice, 1963 b; Norris *et al.*, 1976). The abundance of *B. musculus* relative to other whale species was not expected, as the blue whale has been thought to be an infrequent, transient species in California waters (Rice, 1963 b; Norris *et al.*, 1976; Morejohn, 1977 a). The remaining cetacean species showed a tendency for geometric decline in relative abundance among species (Fig. 2). Similar results were obtained during the second coastal cruise, with *D. delphis* and *B. musculus* again dominating the cetacean fauna (Au, 1980). This dominance pattern is a frequent attribute of ecological communities (McNaughton and Wolf, 1970) and may have utility in assessing the status of disturbed biomes. Dominance may arise from "niche preemption" competition in a species guild whose ecology is dominated by some single factor (Whittaker, 1972; May, 1975). For cetaceans off California, this factor may well be the suitability of the physical environment dominated by lateral and vertical mixing processes. Variation in the pigment content of mesoscale water-masses is related to this mixing and may be associated with differences in prey availability.

The contrasts in distribution, morphology and behavior between *Delphinus delphis*, *Phocoenoides dalli* and even *Lagenorhynchus obliquidens* (for which few schools were seen) may be examples of niche separation on the basis of foraging differences. There are large populations of *D. delphis* in the subtropics and large populations of *D. dalli* in the subarctic. California waters represent range extensions where these two populations meet and overlap. *D. delphis* was widespread in the outer coastal and oceanic waters off California. On the second marine mammal cruise, *D. delphis* were encountered on some of the farthest legs offshore (out to 300 km). However, they appeared not to have been attracted by seamounts. Fishing observers aboard albacore boats have also reported this species in offshore oceanic waters, in one case 375 km from the coast (M. Laurs, unpublished data). *D. delphis* feeds opportunistically (Evans, 1975), although with a preference for mesopelagic prey (Fitch and Brownell, 1968). It is diurnally active and may form large schools. *D. delphis* is often associated with other species, notably *Lagenorhynchus obliquidens*, *Lissodelphis borealis* and the pinniped *Zalophus californianus*, which are all species that also form large aggregations (Leatherwood and Walker, 1977). Although the species appears to travel widely, seasonal migration is apparently not pronounced (Norris *et al.*, 1976). On the other hand, the morphologically different *P. dalli*, perhaps the third most abundant cetacean off California (Rice, 1963 a), was abundant only in the northern survey area and apparently prefers the structurally complex coastal water having high and varying chlorophyll levels (Figs. 1 and 6). This species also feeds opportunistically on squids and schooling fish (Kajimura *et al.*, 1980), may be capable of extra deep diving (Ridgeway and Johnston, 1966), and may feed at night (Morejohn, 1977 b). *P. dalli* schools were small (averaging 5 to 6 individuals) in our study (Table 2), and were not with other dolphins. The species may not travel widely in its daily foraging, although its seasonal distributional changes are conspicuous (Brown and Norris, 1956; Brownell, 1971; Norris *et al.*, 1976; Morejohn, 1977 b), and may be determined in part by the seasonal movements of water masses.

The dissimilarities between these delphinids suggest a strong environmental effect upon their ecology, an effect directly related to the contrasting nature of coastal and oceanic waters. The latter is a less productive habitat, where animals may be less specialized (MacArthur, 1972; Pianka, 1976), more far ranging in their foraging, and likely to form larger and more complex social groupings. On the other hand, species of productive habitats can "afford" to be more specialized and some may tend to occur in smaller groupings. These distinctions may explain the differences between *Delphinus delphis* and *Phocoenoides dalli*, and may be analogous to the ecological differences seen between primates (e.g. baboons) from sparse, resource-limited savanna and from productive forest (Crook, 1970).

A similar speculation would be premature for the species of whales, considering the relatively small numbers encountered. We may point out however, that the *Balaenoptera musculus*, a very specialized "swallowing" feeder of krill (Nemoto, 1970) was encountered in greater concentration in two general areas where increased biological production is typical, i.e., the vicinity of Tanner-Cortez Banks and the Pioneer Seamounts. Similarly, humpback whales feed on krill and a variety of small fishes (anchovies, sauries, sardines) and were sighted in green, high-chlorophyll waters. The fin whales also feed on small fishes in addition to krill but tend to be somewhat more cosmopolitan in distribution.

Phytoplankton, as measured by chlorophyll content, and Cetacea represent the opposite ends of the marine food web. Co-occurrence would suggest that the distribution of organisms that comprise the intermediate levels of the food web are also tied closely to the distribution of primary productivity. Our observations suggest that the thin ribbons of increased biomass along fronts or streamline intersections are exploited by foraging cetaceans. Coastal fronts are often characterized by an enrichment of phytoplankton seaward of the front at shallow depths (Mooers, 1978). These features might explain our observation that cetaceans frequently occurred seaward of the first frontal zone between coastal and nearshore waters. Tilting and subsequent shallowing of the mixed-layer near-fronts could also increase the availability of food to foraging mammals.

The general importance of bottom topography to cetaceans is unclear. Most cetaceans encountered in this study were well offshore of the continental slope. In the Southern California Bight, the complex topography makes it difficult to generalize about topographic effects. We suspect that increased turbulence and the extension of coastal water with increased phytoplankton biomass, e.g. as in the Southern California eddy system (Owen, 1980), are the main reasons for reported relationships between cetacean concentrations and topography (Rice, 1963 a; Evans, 1975; Hui, 1979).

The Coastal Zone Color Scanner (CZCS), an instrument aboard the Nimbus 7 satellite, was especially designed to measure oceanic chlorophyll levels, and hence provides information on the mesoscale features of coastal waters. Figs. 6 and 7 are satellite images from the CZCS taken during the cruise period. They show the richness of detail and the spatial complexity of this marine environment, and illustrate the potential of the satellite for studying living marine resources. By conventional methodology, random sampling, irrespective of species subhabitats, produces population estimates. However, the above cetacean-environment associations suggest that the variations in temperature, salinity and chlorophyll-pigment levels can delimit species habitats in order to improve such estimates. For instance, an appropriate sampling strategy could be developed for enumerating species strongly associated with frontal areas. Real-time satellite imagery could direction ship and/or aircraft sampling to these highly productive and highly variable, limited areas, optimizing search patterns and the statistical data therefrom. The upwelling and frontal, high-chlorophyll areas in Fig. 7 comprise less than 10% of the total area, yet between 20 and 30% of the sightings were in, or in close proximity to, these waters. Thus, the satellite images allow these highly dynamic and relatively small areas to be identified and sampled, and their areal extent, as a function of time, to be quantitatively determined.

To the extent that the abundance of selected cetaceans can be shown to have statistically significant associations with habitat descriptors, more reliable estimates of their distribution and abundance can be made using contemporaneous ship and satellite data. The synoptic overview provided by satellites also enhances the understanding of the dynamics and scale of the biological and physical features characterizing the habitats of Cetacea. This may lead to a more fundamental understanding of cetacean ecology and evolution.

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Transmission electron microscope observations of C-banded skipjack tuna chromosomes

Y. C. SONG*, F. J. RATTY† AND R. M. LAURS‡

**San Diego State University, San Diego, CA 92182, U.S.A. and Wuhan University, Wuhan, People's Republic of China.*

†San Diego State University, San Diego, CA 92182, U.S.A.

‡National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 92038, U.S.A.

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C-banded mitotic chromosomes of *Katsuwonus pelamis* (Linnaeus) were examined by transmission electron microscope (TEM) and results compared with light microscopy images. Advantages of the TEM technique are noted.

I. INTRODUCTION

Electron microscopy is a powerful technique used in chromosome studies on humans (Christenhuss *et al.*, 1967) and other mammals (Kingsley-Smith, 1970). However, there have been very few studies of fish or other lower vertebrate chromosomes using electron microscopy. Webb (1974) was the first to report using scanning electron microscopy on fish chromosomes in an investigation of the karyology of the gobiid teleost *Pomatoschistus minutus*. In the present study we examined C-banded mitotic chromosomes of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus), using transmission electron microscopy (TEM) and have compared the results with light microscopy (LM) images. Our work was patterned after that of Xu & Wu (1983) who conducted comparative studies of LM and TEM images of G-banded human mitotic chromosomes and successfully karyotyped them using the technique developed by Wu & Waddell (1982).

II. MATERIALS AND METHODS

The blood samples from skipjack tuna were collected from freshly caught specimens, the lymphocytes were isolated on a density gradient of ficoll and sodium diatrizoate (Boyum, 1968) and the samples were cultured at 26° C in marine teleost medium (Michael & Beasley, 1973). After 3–5 days cells were harvested, arrested in metaphase with colcemid and placed on slides for C-banding. A detailed description of the methods used is given in Ratty *et al.* (in press).

After the C-banding was completed each field of chromosomes was examined under LM and TEM, using procedures similar to those developed by Xu & Wu (1983). Chromosome preparations were coated with a thin layer of Parlodion by dipping the slide into a stock solution of 0·7% Parlodion in amyl acetate. The edges of the coated slides were scored to free the Parlodion films and 75-count copper grids were placed over selected chromosome complements with the aid of a phase contrast microscope. The Parlodion films with the superimposed grids were then carefully floated off the slide onto the surface of an aqueous solution of 0·01 M hydrofluoric acid. The grids were reexamined

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with phase contrast microscopy to select suitable chromosome complements. The preparations selected were air-dried, stained with saturated uranyl acetate in 50% ethanol for 8 min, and air-dried again. Chromosomes were examined at 50 kV with an RCA EMU-3H electron microscope and the TEM images were recorded on 4489 film. Direct comparisons were then made of the chromosome complements in the LM and TEM images.

III. RESULTS

Light microscopy and TEM images of C-band patterns are presented in Fig. 1: they show that the skipjack tuna has 48 telocentric chromosomes, which is in agreement with the observations reported by Ratty *et al.* (in press). Figure 2 is a karyotype of C-banded chromosomes constructed from the LM and TEM images given in Fig. 1: it shows that the distributions of C-banding on corresponding chromosomes are identical in the TEM and LM images, e.g., chromosome pairs 1, 2, 4, 6, 15, and 21 have the same prominent centromeric C-bands in both images. While the C-banding patterns are the same in the LM and TEM images, considerably greater detail is apparent in the TEM images. For example, chromosome fibres are visible in the TEM images, but not in the LM images. Figure 3 shows the fibres for chromosome pairs 2, 15, and 24 at 1800X magnification. The fibres are discernible in the centromeric regions and in the arms of the chromosomes where they form diffuse boundaries. The size of the fibres is uniform among chromosomes of varying size and measures about 300 ångströms, which is consistent with the observations of Harrison *et al.* (1981) and Harrison *et al.* (1983) for human chromosomes observed under SEM.

The TEM images also show a multiple banding pattern in addition to the C-bands on some chromosome pairs, e.g., 1, 2, 4, 6, 15, and 21 (Fig. 2). The bands in pairs 2 and 15, shown in Fig. 3, correspond to ridges while the interband regions appear as depressed grooves. The multiple banding pattern was not apparent in the LM images.

In the TEM images the centromeric C-bands all appear as darkly stained bands of uniform width, while in the LM images the centromeric C-bands of the corresponding chromosomes appear irregular in width with prominently stained swollen knobs. In addition, some chromosome regions appear as lightly stained gaps in the LM images, whereas the same chromosome region observed in the TEM images is actually morphologically continuous.

IV. DISCUSSION

Our results show that the TEM technique developed by Wu & Waddell (1982) for investigating human chromosomes has significant advantages over LM in studying fish chromosomes. The high number and the extremely small size of chromosomes of many fish species make it difficult to investigate the karyology of fishes. Using TEM images it is possible to study the complete set of diploid chromosomes and to analyze chromosome complements of cells with a high degree of resolution not possible with LM. For example, the greater resolution of TEM made it possible to distinguish chromosome fibres, which allowed us to readily discriminate small chromosomes and chromosome satellites from stain particle artifacts, which under LM sometimes resembled small chromosomes.

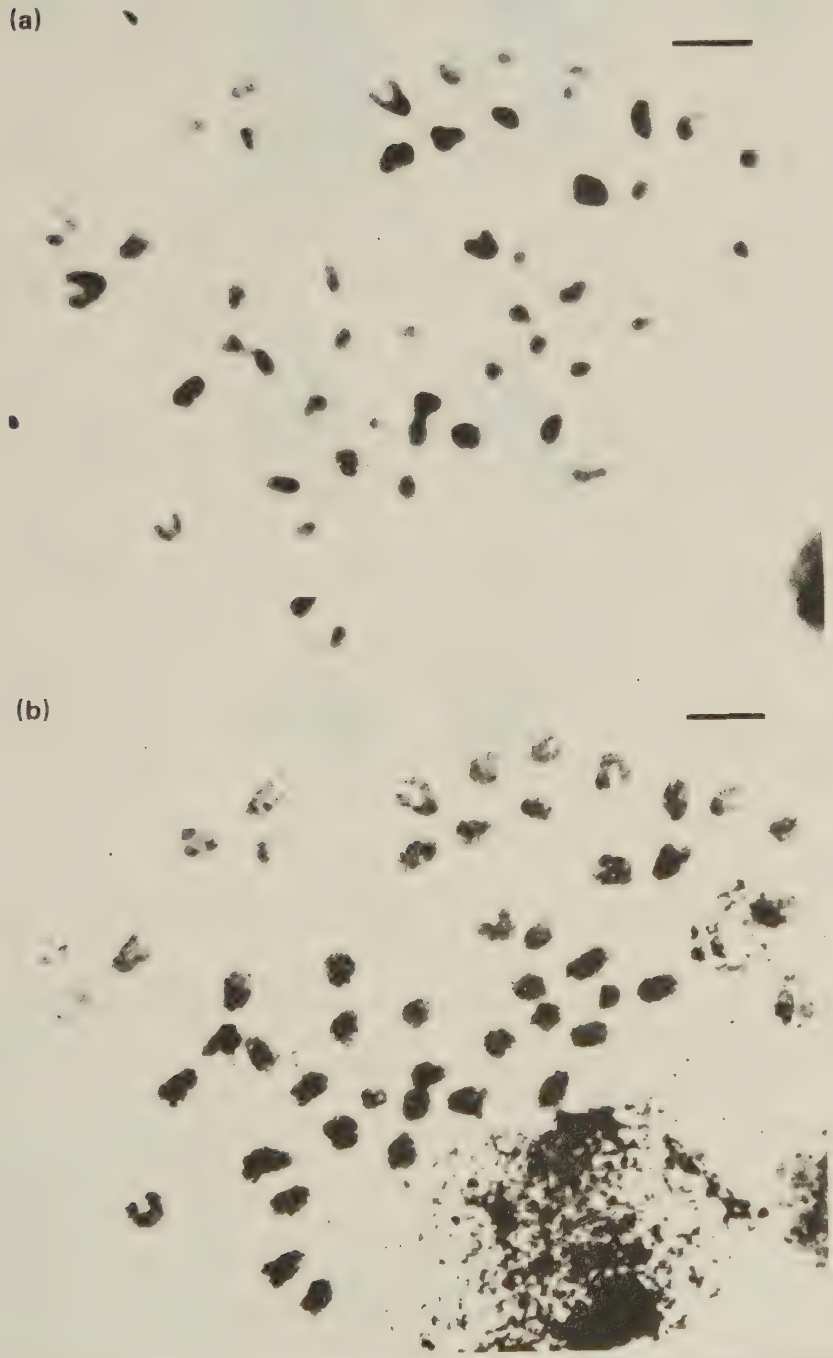

FIG. 1. Comparison between light microscopic images and transmission electron microscopic images of the same C-banded metaphase chromosomes in skipjack. $2n = 48$. (a) Light micrograph. (b) Electron micrograph. Scale indicates 2μm.

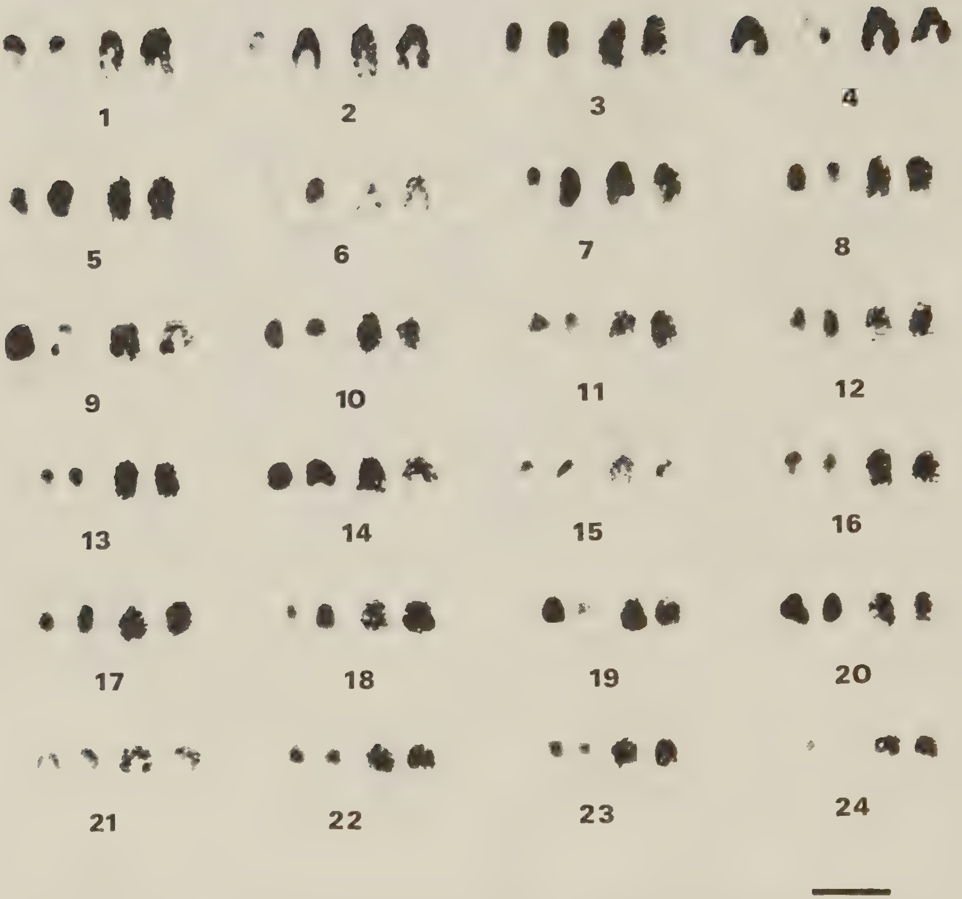

FIG. 2. C-banding karyotype of skipjack, using transmission electron microscope micrographs. 2n = 48. For each pair of chromosomes, light micrographs (left) are included for comparison. Scale indicates 2μm.

According to Dupraw (1970), Golomb (1976) and Bahr (1977), fibres are present in chromosomes but are not associated with stain particles. The use of TEM has confirmed that all of the skipjack chromosomes are telocentric. Ratty *et al.* (in press) reported that skipjack tuna chromosomes were probably all telocentric, although some of the chromosomes observed under LM resembled subtelocentrics. The discrepancy between LM and TEM observed in some chromosomes probably is due to differences in staining properties. Giemsa staining, which is used in LM, results from side stacking of thiazine dyes on DNA and the accumulation of dye at the bands (Blakey & Filion, 1967; Cervenka *et al.*, 1973; Ross & Gormley, 1973). Excessive accumulation of dye could be the reason for the subtelocentric appearance of chromosomes observed under LM. This is not a problem when chromosomes are stained with uranyl acetate for TEM, since only the density changes and the morphology of the chromosome is accurately preserved. While Giemsa was used in our C-banded preparations, it was inactivated following treatment with uranyl acetate (Xu & Wu, 1983).

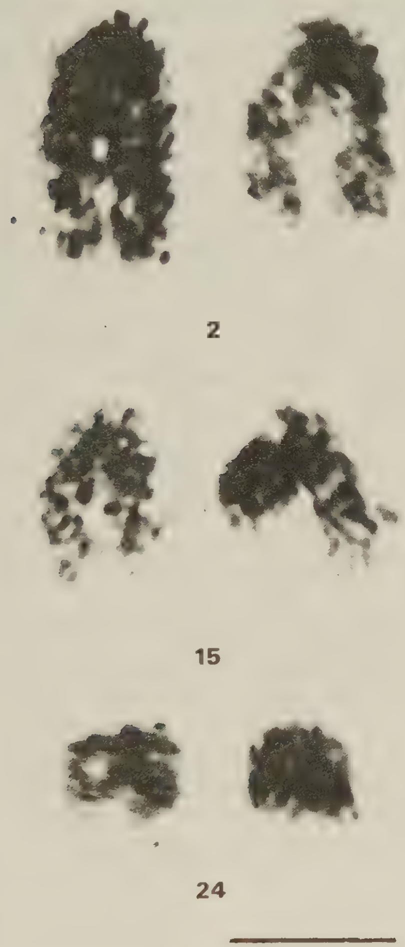

FIG. 3. Electron micrographs of chromosome pairs 2, 15 and 24 of skipjack. Scale indicates 1µm.

The banding we observed under TEM in addition to C-bands may possibly be G-bands. The multiple band and interband regions that we observed on some of the chromosomes is similar to the description of G-banding observed in SEM images by Utsami (1982). It also corresponds to G-bands observed in human chromosomes treated with trypsin and examined under TEM by Xu & Wu (1983). If the ridge and groove patterns we observed are actually G-bands, the TEM techniques of Xu & Wu (1983) may provide a mechanism for studying G-banding in fish for which ideal methods have yet to be established.

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EX-VESSEL PRICE LINKAGES IN THE NEW ENGLAND FISHING INDUSTRY

DALE SQUIRES[1]

ABSTRACT

This study examines the direction of ex-vessel price linkages between the three New England ports of Boston, New Bedford, and Gloucester. Within-sample, bivariate tests of Granger causality are applied for monthly data from 1965 through 1981. It is found that cod and haddock prices are formed in New Bedford, that pollock prices are simultaneously formed between Boston and Gloucester, and that a spurious relationship exists for flounder prices between the three ports. The hypothesis is advanced that this spurious relationship may be due to flounder price leadership from outside the region, most probably the New York Fulton Fish Market.

The direction of price linkages between various market and production centers in an industry is important to studies of marketing and prices. Although these spatial and hierarchical relationships are generally well understood in domestic agriculture, they have received little or no attention in natural resource utilization and in the domestic commercial fishing industry in particular. This study therefore examines the spatial characteristics of round ex-vessel price linkages of the most important species in the New England fishing industry from 1965 through 1981.

Three ports—New Bedford, Boston, and Gloucester—dominate the New England fishing industry, as both home ports or production centers and as marketing centers. By both volume and value of landings, New Bedford is the most important port, followed by Gloucester and then Boston. The most important species of groundfish in New England are cod; haddock; yellowtail, winter, and other flounders; ocean perch or red fish; and pollock. Sea scallops and lobsters also provide a significant contribution to the industry in both value and volume of landings. This study accordingly focuses upon the ports of Boston, New Bedford, and Gloucester, and the species of cod, haddock, yellowtail and winter flounders, and pollock. Additional attention is given to ocean perch and sea scallops, though rigorous conclusions are not possible.

In New Bedford and Boston, fishermen sell their catches to the highest bidder in an open auction. The New Bedford auction begins at 8:00 a.m. and ends at 8:22 a.m. The Boston market begins at 7:00 a.m., and invariably overlaps with the New Bedford market. There is significant communication between the two markets during the auctions. The volume and total value of fish harvested is substantially greater in New Bedford than in Boston. Bidders purchase an entire vessel's landings in New Bedford, while in contrast, purchasers offer individual bids for each species in Boston. In most of the ports other than Point Judith in Rhode Island (where an important fishermen's cooperative exists), the catch is sold directly to fish processors or by prior arrangements between individual vessels and purchasers. Further, it is generally believed that Gloucester prices for most fresh groundfish species are set in Boston, and differ only by a transportation cost.

Fishermen of all ports are free to land their harvests at any port offering the highest prices, which, however, must be balanced against steaming time. Few vessels land exclusively at a single port, since the distances between the three are not great. A definite limit exists to port switching due to the prevalence of market transactions costs. Wilson (1980) indicated that personal and financial relationships tend to bind particular fishermen and fish buyers. In contrast to many other natural resource and primary production industries, a futures market does not exist for fresh fish.[2]

Different ports and markets have developed singular reputations. These specializations are based in large part upon proximity to resource stocks. New Bedford has developed a reputation as a flounder and sea scallop port, while Boston has become known as a cod, haddock, and, to a lesser extent,

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2] Trading on futures markets involves buying and selling standardized contracts for the future delivery of a specific grade of a commodity at a specific location(s).

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pollock port. Although Gloucester fishermen direct much of their effort towards cod, haddock, and flounders (generally joint products), Gloucester has developed a reputation as a port for both pollock and ocean perch.

Conventional wisdom in the New England groundfishery market holds that New England round (fish as harvested) ex-vessel prices of fresh flounders are formed in the New Bedford auction market, while fresh cod, haddock, and pollock round ex-vessel prices are set in the Boston auction. These widely held beliefs serve as the null hypotheses to be tested in this study of the ex-vessel groundfish price linkages in New Bedford, Gloucester, and Boston.

Knowledge of ex-vessel price linkages has a number of applications. Efforts at improving market efficiency would find this information useful. The broadcasting of daily ex-vessel fish prices by the National Marine Fisheries Service can properly focus upon the most crucial markets. Infrastructural or institutional improvements can be more judiciously targeted, an important consideration in a time of tight public and private budgets. Price forecasts to improve industry functioning can concentrate upon those prices formed in markets which demonstrate price leadership. Fishermen may want to land their harvests in the market in which ex-vessel prices are first formed, should fishermen want to affect the pricing process, be less dependent upon the landings of others, or capture advantageous prices. Similar considerations apply to buyers. Knowledge of the price formation process allows government price policies to target the appropriate markets. Finally, price linkage information is crucial to studies of marketing margins, length of price transmission, and asymmetric pricing.

THE DATA

The data are taken from the vessel weighout files of the National Marine Fisheries Service. After every trip of a commercial fishing vessel of any gear type, port agents in each port obtain the value and volume of landings for each species harvested. The entire collection of this information constitutes the weighout file. The output vector from the weighout file is then linearly aggregated over vessels and trips to form monthly round ex-vessel prices for each port. The resulting nominal prices are subsequently deflated by the consumer price index for food. As Sims (1974) and Feige and Pierce (1980) noted, the use of seasonally adjusted data may confound lag distributions and causality relationships. Consequently, the data are left in their unseasonalized state. However, to account for seasonal differences, quarterly dummy variables are employed. The time domain of the data set extends from 1965 through 1981.

METHOD OF ANALYSIS

Granger (1977) provided a definition of causality among a set of variables that is based upon predictability as well as the fact that the effect of a change in an exogeneous variable upon an endogeneous variable requires time. A variable X causes another variable Y, with respect to a given universe or information set that includes X and Y, if present Y can be better predicted by using past values of X than not doing so, all other information in the past of the universe being used in either case. Causality from Y and X is defined in the same manner. Feedback occurs if X causes Y and Y causes X. A causal relationship between X and Y does not exist if causality does not run from X to Y or from Y to X, and feedback does not occur.

Causality tests may be classified into two fundamental types at their most basic level, within-sample and out-of-sample tests. The within-sample test is widely applied and is the first one developed. This test is developed over the full-time domain of the data set, and essentially relies upon a measure of fit. The definition of causality in the out-of-sample test requires evidence of improved forecasts. This approach is implemented by identifying and estimating different models using the first part of the sample and then comparing their respective forecasting abilities on the latter part of the sample. This study utilizes the within-sample test, the one most commonly applied, since the properties of the out-of-sample test have yet to be systematically examined.

Two basic approaches have been advanced by which to apply empirically the within-sample bivariate Granger criterion to time series. The first approach is represented by the test proposed by Pierce (1977) based upon Haugh (1976). The procedure first estimates whitening filters for each time series, then subsequently estimates the cross-correlation function for the first step's residuals.[3] However, Sims (1977) and Geweke (1981) indicated that this approach may be limited.[4] A second basic approach relying directly upon distributed lag relationships between dependent and independent variables has led to three widely used tests: those suggested by Sims (1977), the direct Granger test forwarded by Sargent (1976), and the Modified Sims test advanced by Geweke et al. (1983).

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[3] Whitening filters remove serial correlation from a time series. Each time series used in a test of causality will be a white noise process, and any relationships will be based on actual, systematic relationships between the two time series, instead of a spurious relationship caused by the common serial correlation.

[4] Prefiltering each time series with separate autoregressive integrated moving average (ARIMA) filters biases the test toward

The small-sample properties of the Sims (1972), direct Granger, and Modified Sims tests have recently been examined within Monte-Carlo frameworks by Guilkey and Salemi (1982) and Geweke et al. (1983). Although the two studies differ somewhat in their specifications, both found that the Sims test was outperformed by the other two. Since the Sims test is more time-consuming and expensive to employ and requires more decisions about parameterizations, both studies unequivocally recommend against its use.

The two studies reach slightly different conclusions on the efficacy of the direct Granger and Modified Sims test. These contradictory results can be attributed to differences in research design. Geweke et al. (1983) concluded that the two tests essentially perform equally well. In contrast, Guilkey and Salemi (1982) determined that the direct Granger test consistently outperforms the Modified Sims procedures by small amounts. Since the direct Granger test is computationally the least expensive of the three and results in the fewest degrees of freedom lost from formation of leads and lags, Guilkey and Salemi recommend its use over the Modified Sims and Sims procedures. Nonetheless, they do note that the Granger procedure's advantage over the other two diminishes with increases in sample size.

Several additional findings of Guilkey and Salemi (1982) are also worth reporting. They observed that for sample size <200, the shorter versions of all three tests are superior to the longer versions.[5] They further noted that in their Monte-Carlo study the direct Granger and Modified Sims procedures accurately recover the coefficients of the relevant population projections of the statistical model used to generate experimental time series in small samples. Consequently, it may be unlikely to observe "large" coefficient estimates arising spuriously. Finally, test performance is extremely sensitive to sample size, strength of causation, and length of test parameterization employed.

The direct Granger test as applied in this study is based upon ordinary least squares regression of the current observation of the time series of round ex-vessel prices from one port upon its own past observations and the past observations of the other port's round ex-vessel prices for species k:

$$P2_k(t) = a_k + \sum_{i=2}^{4} b_{ki} D_i + cLT + \sum_{j=1}^{J} d_{kj} P2_k \times (t - j) + \sum_{j=1}^{J} f_{kj} P1_k (t - j) + e_{kt}. \qquad (1)$$

Here, LT refers to a linear time trend, D_i is the zero-one variable for quarter i, $P1_k(t)$ is the round ex-vessel price of species k in month t in port 1, J is the number of periods lagged, and e_{kt} is a vector of stochastic, white noise residuals. The presence of lagged dependent variables in Equation (1) is counted on to remove serial correlation from the estimated residuals.[6]

The test of the null hypothesis that $P1_k$ does not cause $P2_k$ is a test that $f_{kj} = 0$, $j = 1,2,\ldots,J$. Guilkey and Salemi (1982) indicated that the F-test statistic is calculated by estimating Equation (1) in both constrained ($f_{kj} = 0$, $j = 1,2,\ldots,J$) and unconstrained forms, and may be written as[7]

$$F = \frac{(SSE_c - SSE_u)/J}{SSE_u/(T - (2J + 2))}, \qquad (2)$$

where SSE_u and SSE_c are the residual sum of squares from the unconstrained and constrained regressions, respectively, and T represents the number of monthly observations on round ex-vessel prices. Under the null hypothesis, F is an F-test statistic with J and $T - (2J + 2)$ degrees of freedom. This procedure is then repeated reversing the roles of $P1_k$ and $P2_k$ to test the null hypothesis that $P1_k$ does not cause $P2_k$.

The direct Granger test requires selection of a lag length, J, large enough to purge serial correlation from estimated residuals. Several factors require consideration before specifying the lag length. Chilled fresh fish is a commodity that rapidly deteriorates in quality. Consequently, definite limits exist to the length of time which inventories of

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failing to reject the null hypothesis of independence of the two series more often than the specified level of significance suggests. Because of this limitation, the second basic approach is applied.

[5] Longer versions of these tests include additional lead and lag variables.

[6] Serial correlation exists when the error terms from different observations in a time series are correlated. Serial correlation tends to give unbiased but inefficient estimators, and a biased sampling variance, which then affects the results from significant tests such as the F- or -t-tests.

[7] A constrained F-test includes one or more restrictions, such as one or more coefficients constrained to zero. An unconstrained F-test does not include these restrictions.

chilled fresh fish can be held. Since most groundfish harvested in New England waters are not processed into frozen fish products, long-term storage of New England groundfish is unlikely, and fresh fish prices are likely to adjust more quickly than those of most other food commodities. In addition, previous exploratory analysis with adaptiver filtering methods on the weighout file suggests that two sets of round ex-vessel prices for any species k are particularly important, the previous month's price and the price within one month on either side of the previous year. In order to account for these characteristics and to provide both short and long versions of the test, lags of 8 and 14 mo were specified. These lag lengths are sufficiently long to encompass price lags with monthly data. The diagnostic Q test of Box and Pierce (1970) is used to detect serious serial correlation.

EMPIRICAL RESULTS

The empirical results from the direct Granger causality tests lead to somewhat unexpected conclusions for most species. The null hypothesis that monthly round ex-vessel prices of cod and haddock in all three ports are first formed in the Boston auction market is rejected in almost all instances. The findings in Table 1 instead suggest that the cod and haddock prices established in the New Bedford auction lead the prices formed in the Boston market. Several factors may account for this. The New Bedford auction's volume of landings is substantially higher than that of Boston. In addition, the two market times ordinarily overlap, and frequent communication occurs between economic agents during the auctions. Further, the proximity of New Bedford to Boston allows fresh fish to be easily trucked to Boston from New Bedford. The markets are thus physically linked, before the auctions by fishermen and after the auctions by fish buyers. One element of conventional wisdom may perhaps be substantiated, however. Although the Q-test statistic indicates severe serial correlation (and thereby possibly refuting the F-test statistic), the empirical results indicate that Boston cod prices do lead Gloucester cod prices at the ex-vessel level for the shorter lag length parameterization.

Rejection of the null hypothesis that Boston prices lead New Bedford and probably Gloucester cod and haddock round ex-vessel prices and the finding that New Bedford prices lead Boston prices suggest a second null hypothesis for consideration. This second hypothesis states that Gloucester cod and haddock prices are directly led by New Bedford prices. In addition, the possibilities that Boston prices lead Gloucester prices and that New Bedford prices lead Boston prices suggest an additional, indirect price linkage between Gloucester and New Bedford via Boston.

The results for this second null hypothesis are also given in Table 1. Since this is an unplanned comparison, a Scheffe interval is used.[8] Strictly followed,

TABLE 1.—Direct Granger causality tests for monthly fresh round ex-vessel cod and haddock prices.

Cod				Haddock			
Direction[1]	Lags[2]	F-test[3]	Q-test[4]	Direction[1]	Lags[2]	F-test[3]	Q-test[4]
B --------->G	8	2-37*	35.67*	B --------->G	8	1.69	9.60
B --------->G	14	1.17	2.61	B --------->G	14	1.09	4.49
G --------->B	8	1.59	10.98	G --------->B	8	1.07	10.98
G --------->B	14	1.02	12.35	G --------->B	14	1.29	15.07
B --------->NB	8	1.67	13.52	B --------->NB	8	0.08	12.54
B --------->NB	14	0.74	21.85*	B --------->NB	14	0.09	7.06
NB --------->B	8	2.52*	8.82	NB --------->B	8	3.15*	8.62
NB --------->B	14	1.89*	16.27	NB --------->B	14	1.76*	8.74
G --------->NB	8	1.78	16.46	G --------->NB	8	0.56	11.71
G --------->NB	14	0.91	28.42	G --------->NB	14	1.36	15.09
NB --------->G	8	[5]2.96	7.84	NB --------->G	8	[5]2.90	11.76
NB --------->G	14	1.40	6.86	NB --------->G	14	1.65	8.37

[1] Variable abbreviations are B (Boston), G (Gloucester), NB (New Bedford).

[2] J indicates J months lagged.

[3] Null hypothesis that past values of the causal variable do not significantly affect current values of the dependent variable. An asterisk indicates rejection of the null hypothesis at the 5% level.

[4] Null hypothesis that regression residuals are white noise. An asterisk indicates rejection of the null hypothesis at the 5% level.

[5] F-test statistic is significant at the 5% level, but not significant at the 5% level when a Scheffe interval is used.

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[8] An unplanned comparison occurs when in the course of examining results a hypothesis is tested which was not specified prior to the experiment. The initial region is altered by the additional information, so that the level of significance has changed. A Scheffe interval allows for a more cautious test by providing a larger critical value than that given by a t or F table. This pre-test bias is accounted for by a conservative test. The F-test statistic now

the results indicate that the cod and haddock price linkage does not run from New Bedford to Gloucester. If a Scheffe interval is not used, then the New Bedford cod and haddock prices do lead those of Gloucester. Therefore, with this caveat, New Bedford auction market monthly round ex-vessel cod and haddock prices lead the prices of Gloucester and Boston, and Boston prices may lead those of Gloucester. In any case, it appears that the New Bedford auction market dominates the formation of round ex-vessel prices for cod and haddock.

The empirical results for yellowtail and winter flounder of Table 2 also contradict the null hypothesis that monthly fresh round ex-vessel prices for both species are formed first in New Bedford. Instead, the findings indicate that pricing feedback exists between both New Bedford and Gloucester and between New Bedford and Boston. These conclusions must be tempered by the significant *Q*-test statistics for several relationships.

These conclusions lead to a second null hypothesis to be tested on the yellowtail and winter flounder price linkages between Gloucester and Boston. Since this test is also an unplanned comparison, a Scheffe interval is required. Again, the strict test results indicate that neither port's prices lead the other, nor that feedback exists.

TABLE 2.—Direct Granger causality tests for monthly fresh round ex-vessel yellowtail and winter flounder prices.

Yellowtail flounder				Winter flounder			
Direction[1]	Lags[2]	*F*-test[3]	*Q*-test[4]	Direction[1]	Lags[2]	*F*-test[3]	*Q*-test[4]
NB ——>G	8	2.05*	20.19	NB ——>G	8	7.52*	5.68
NB ——>G	14	2.27*	19.42	NB ——>G	14	8.71*	1.78
G ——>NB	8	1.96*	23.56*	G ——>NB	8	2.88*	16.98
G ——>NB	14	2.48*	26.78*	G ——>NB	14	2.97*	22.19*
NB ——>B	8	2.02*	10.56	NB ——>B	8	11.87*	18.45
NB ——>B	14	1.76*	9.89	NB ——>B	14	7.66*	7.92
B ——>NB	8	0.75	17.63	B ——>NB	8	23.57*	9.94
B ——>NB	14	2.83	21.83*	B ——>NB	14	5.25*	3.99
G ——>B	8	2.27[5]	9.41	G ——>B	8	3.87[5]	12.43
G ——>B	14	2.50[5]	12.74	G ——>B	14	4.37[5]	4.70
B ——>G	8	1.48	16.86	B ——>G	8	4.15[5]	18.16
B ——>G	14	1.27	18.82	B ——>G	14	3.56[5]	17.34

[1] Variable abbreviations are B (Boston), G (Gloucester), NB (New Bedford).

[2] *J* indicates *J* months lagged.

[3] Null hypothesis that past values of the causal variable do not significantly affect current values of the dependent variable. An asterisk indicates rejection of the null hypothesis at the 5% level.

[4] Null hypothesis that regression residuals are white noise. An asterisk indicates rejection of the null hypothesis at the 5% level.

[5] *F*-test statistic is significant at the 5% level, but not significant at the 5% level when a Scheffe interval is used.

The most probable explanation for the feedback between the prices of New Bedford and Gloucester, New Bedford and Boston, and possibly between Gloucester and Boston rests with a spurious relationship. Although New Bedford is the most important flounder port by landings in New England, New York City is even more important on the eastern seaboard by volume of consumption. New York City's Fulton Fish Market is primarily a wholesale market without substantial landings. Much of the New England flounder harvested is sent to Fulton on consignment without an ex-vessel price being established in New England. The Fulton Fish Market also begins much earlier in the morning than New Bedford's auction market. Thus the apparent feedback among the ex-vessel yellowtail and winter flounder prices in the New England ports is probably due to their following of the wholesale prices set in the Fulton Fish Market.

Table 3 presents the results for pollock. As with the other species, consistent results are obtained for different lag lengths. Again, the null hypothesis dic-

TABLE 3.—Direct Granger causality tests for monthly fresh round ex-vessel pollock prices.

Direction[1]	Lags[2]	*F*-test[3]	*Q*-test[4]
B ——>G	8	4.34*	12.54
B ——>G	14	4.99*	10.15
G ——>B	8	5.28*	18.27
G ——>B	14	4.77*	22.96*

[1] Variable abbreviations are B (Boston), G (Gloucester), NB (New Bedford).

[2] *J* indicates *J* months lagged.

[3] Null hypothesis is that past values of the causal variable do not significantly affect current values of the dependent variable. An asterisk indicates rejection of the null hypothesis at the 5% level.

[4] Null hypothesis that regression residuals are white noise. An asterisk indicates rejection of the null hypothesis at the 5% level.

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becomes significant only if it exceeds in magnitude $((a\text{-}1)F_b)^{1/2}$, where F is the $b \cdot 100\%$ critical value for $F\ (a\text{-}1, N\text{-}a)$ and N is the number of observations. See Snedecor and Cochran (1976, p. 271) for more details.

tated by widely held industrial perceptions is rejected. The results indicate that feedback exists between the monthly fresh round ex-vessel prices of pollock in both Gloucester and Boston. Both ports dominate pollock landings and are close to one another.

A complete time series of prices for sea scallops exists only for New Bedford. Since New Bedford greatly dominates this fishery by both volume and value of landings, it may be safely concluded that monthly round ex-vessel sea scallop prices are formed in New Bedford. Finally, Gloucester is the only one of these ports to possess a complete time series of prices and landings of ocean perch or red fish. Since Gloucester dominates this fishery, monthly fresh round ex-vessel ocean perch prices appear to be formed in this port, at least among these three.

CONCLUDING COMMENTS

The within-sample bivariate direct Granger causality tests of monthly round ex-vessel price linkages for the three most important New England ports (Boston, New Bedford, and Gloucester) and the most important groundfish species lead to unexpected results. Conventional wisdom considers the round ex-vessel cod and haddock prices formed in the Boston auction market to lead the comparable prices of the other New England ports. However, the empirical results indicate that New Bedford's prices lead those of the other ports, although in certain cases Boston's cod prices may lead those of Gloucester as well.

The common industry perception also holds that the yellowtail and winter flounder round ex-vessel prices are first formed in New Bedford and lead those of Boston and Gloucester. Instead, the empirical findings suggest that feedback and simultaneous price formation occur among all three ports for both species. Since flounder landings in Boston and Gloucester are negligible in comparison to those of New Bedford, a spurious relationship due to the leading wholesale prices formed in the even earlier and more flounder-important Fulton Fish Market of New York City is suggested. Feedback is likely for fresh round pollock ex-vessel price formation in Boston and Gloucester. Finally, it is suggested that the New Bedford auction market dominates fresh ex-vessel sea scallop price formation and that Gloucester dominates among these three ports for ocean perch. New Bedford thus generally dominates ex-vessel price formation among the major New England ports for the most important species harvested.

ACKNOWLEDGMENTS

Helpful comments from David Bessler, Joseph Mueller, Robert Reidman, Patricia Kurkul, and Daniel Huppert and an anonymous reviewer are gratefully acknowledged.

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On the Flying Squid *Stenotuthis oualaniensis* (Lesson) In Hawaiian Waters*

Tsuneyoshi Suzuki**, Shoichi Yamamoto***, Kiyohiko Ishii***
and Walter M. Matsumoto****

Abstract

By the request of Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration (NOAA), the cooperative research of squid species in Hawaiian waters by Hokusei Maru Training ship of Hokkaido University was began from February, 1981, from two years. Furthermore University of Hawaii hopes for continuation of this research from November in 1983, and planned until 1987.

The present results of this research can be summarized as follows.

1) The predominant species of squid distributed in Hawaiian waters was flying squid *Stenotuthis oualaniensis*.

2) Flying squid was male prior mature and size of male smaller than female. In fully maturity, the mantle length of male was about 145～150 mm and female was about 225～230 mm.

3) Relation between the mantle length (Y) to body weight (X) for female was $Y = 0.000018 \times^{3.15} (r^2 = 0.9597)$, and for male was $Y = 0.000042 \times^{2.99} (r^2 = 0.7006)$.

4) In November, immature stage were predominated distribution in Southwest area of Oahu island for both male and female; and three months later in February, in the same area including Southern area of Oahu island was almost unappear.

5) In February, the matured female was concentrated in off Hilo, east coast of Hawaii island. Here was considered as one of the spawning ground of this species, and the spawning season was from February to March.

6) Spawned in off Hilo, during floating period after hatching, they transfered to west-ward by current. The swimming capability increased with growth, they migrate to east-ward reaching again off Hilo spawning ground in February to March. This support our hypothesis.

7) From views of growth and maturity, it is considered that life cycle of *S. oualaniensis* like of other squid of the same family is one year.

8) Flying squid widely distributed in mid-Pacific ocean and Indian ocean. Off Hilo as one of the spawning ground might be indicated that subpopulation of flying squid exist in waters adjacent Hawaiian Islands.

Introduction

To obtain the information of squid species in Hawaiian waters, its ecology and assessment of the resources, Honolulu Laboratory, Southwest Fisheries Center,

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** *Laboratory of Instrument Engineering for Fishing, Faculty of Fisheries, Hokkaido University.*

*** *Hokusei Maru Training Ship, Faculty of Fisheries, Hokkaido University.*

**** *Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, NOAA*

National Marine Fisheries Service, NOAA, requested the cooperative research with Hokkaido University. The agreement of the cooperative research for along three years and was began in February, 1981. Furthermore, University of Hawaii hope for continuation of this research from November, 1983 and planned until 1987. This report describes the present results of this research, particularly distribution,

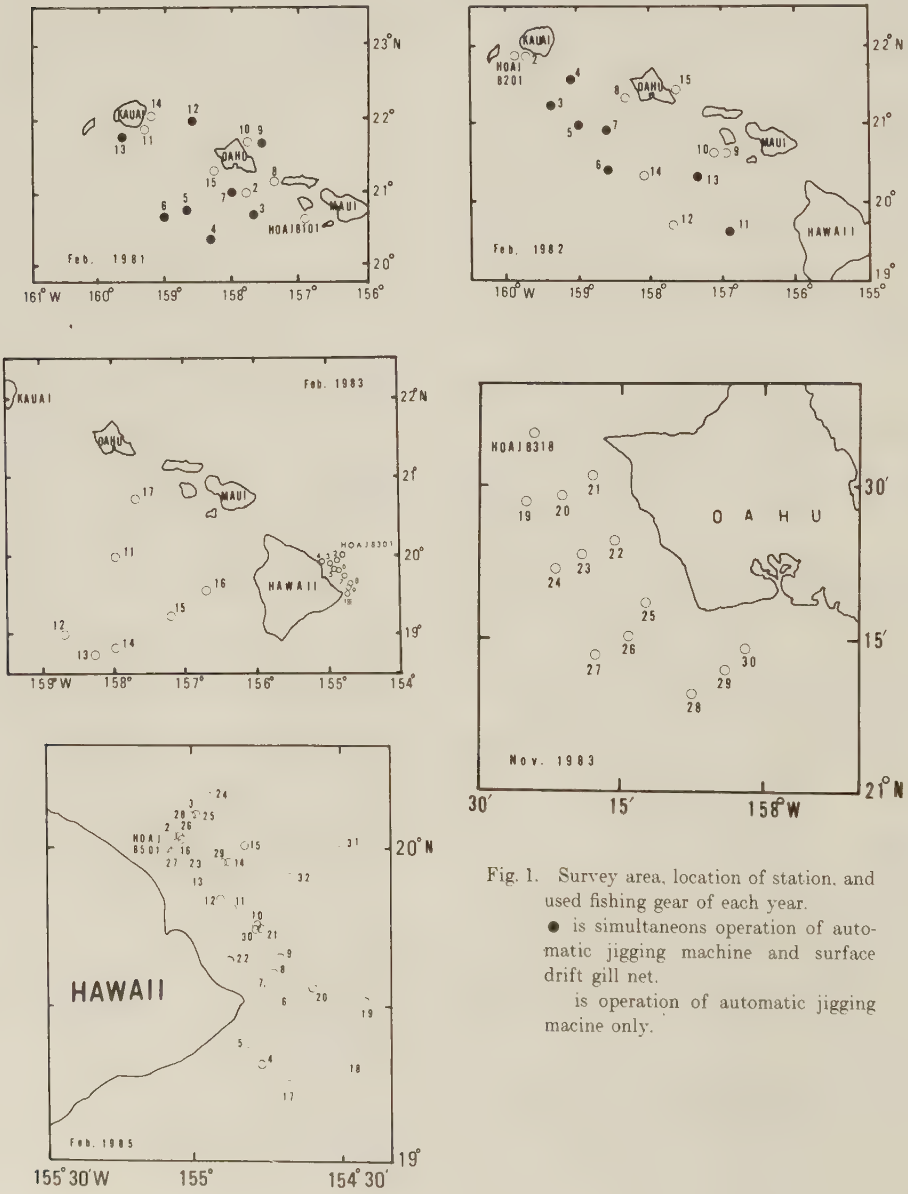
Feb. 1981
KAUAI
OAHU
MAUI
HOAJ8101
23°N
22°
21°
20°
161°W
160°
159°
158°
157°
156°
Feb. 1982
KAUAI
HOAJ 8201
OAHU
MAUI
HAWAII
22°N
21°
20°
19°
160°W
159°
158°
157°
156°
155°
Feb. 1983
KAUAI
OAHU
MAUI
HAWAII
HOAJ8301
22°N
21°
20°
19°
159°W
158°
157°
156°
155°
154°
Nov. 1983
HOAJ 8318
O A H U
30′
15′
21°N
30′
15′
158°W
Feb. 1985
HAWAII
HOAJ 8501
20°N
19°
155°30′W
155°
154°30′

Fig. 1. Survey area, location of station, and used fishing gear of each year.
● is simultaneons operation of automatic jigging machine and surface drift gill net.
is operation of automatic jigging macine only.

growth, sex ratio of flying squid *S. oualăniensis* and propose a hypothesis of their life history.

Materials and Methods

The survey was carried out in February for every years with the exception of in 1983 the survey also conducted in November other than in February. The term of survey and used fishing gear are given in Table 1, and survey area and location of stations are shown in Fig. 1.

Fishing gear used in this survey were a double system automatic squid jigging with three machines, one line consisting of 30 squid jigs placed one meter apart and surface drift gill net with 18 kinds of mesh size and total 79 shackles. The mesh size, shackle number of used surface drift gill net and its construction are shown in Table 2.

The survey area was designed to cover of the all waters adjacent to Hawaiian waters except those due to bad weathers.

Table 1 Survey term and fishing gear used for each year

Year	Survey term	Fishing gear
1981	27 Jan. to 12 Feb.	Surface drift gill net and automatic jigging machine
1982	26 Jan. to 12 Feb.	〃
1983	5 Feb. to 21 Feb.	〃
1983	26 Nov. to 3 Dec.	Automatic jigging machine
1985	2 Feb. to 20 Feb.	〃

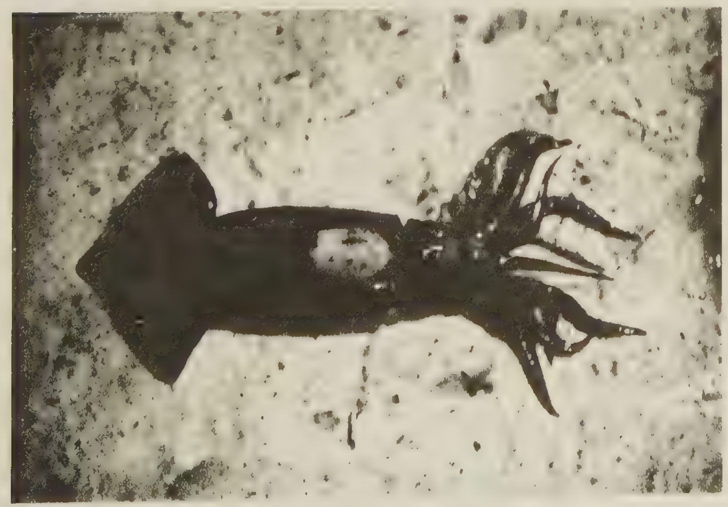

Fig. 2. Photograph of *S. oualaniensis*

Results

The species of squid captured by surface drift gill net were tobi-ika *Stenotuthis oualaniensis* (Lesson), aka-ika *Ommastrephes bartrami* (Lesueur), tsume-ika *Onychoteuthis banksii* (Leach), Hawaisurume *Nototodares sloani hawaiiensis* (Berry). Because very few number in all catch of surface drift gill net, only data of flying squid *S. oualaniensis* captured by automatic squid jigging machine was investigated[1)2)].

Stenotuthis oualaniensis (Lesson) is species of living in open sea[3)], widely distributed from equatorial waters including Indian Ocean extenting to mid-North and mid-South Pacific Ocean. Morphologically similar to Japanese common squid

Table 2 Mesh size and shackle number of surface drift gill net and its construction

Mesh size	Shackle number	Mesh size	Shackle number
Stray net			
121	5	121	3
48	3	37	6
25	6	72	3
93	3	159	3
55	3	42	6
29	6	82	3
138	3	179	3
106	3	204	3
33	6	233	3
63	3	Stray net	
		121	5
		Total	79

Table 3 Fishing ground, catch of *S. oualaniensis*, ratio of female to

Year	Fishing ground	Catch	Female-male ratio (%)
1981. Feb.	Oahu Is. South	400	75 : 25
1982. Feb.	〃	131	79.4 : 20.6
1983. Feb.	〃	146	72.6 : 27.4
1983. Feb.	Hawaii Is. East	533	81.2 : 18.8
1983. Nov.	Oahu Is. West	760	75.9 : 24.1
1985. Feb.	Hawaii Is. East	369	81.1 : 18.9

※ Maturity 1 is immature stage, maturity 3 is matured stage

Todarodes pacificus Steenstrup, classifying in family Ommastrephidae and has a special feature that is big photo organ at dorsal as shown in Fig. 2.

Table 3 shows the fishing ground, catch of flying squid *S. oualaniensis*, ratio of female to male, mean mantle length, mean body weight, and maturity of each year. Mean CPUE (catch per unit jigging machine per one hour) and its confidence intervals of each year are given in Table 4.

Figs. 3 (a) and (b) shows histogram of mantle length (a) and body weight (b) of *S. oualaniensis* female in the waters south of Oahu island. The histogram of male are given in Figs. 4 (a) and (b). The composition in south and southwest of Oahu island has approximately same trend in February, 1981, 1982, and 1983, only 1981 was showed as model.

The histogram of mantle length (a) and body weight (b) of *S. oualaniensis* female and male in waters east of Hawaii island in February, 1983 are given in Figs. 5 (a) and (b); and Figs. 6 (a) and (b) respectively. Data obtained from the same waters in February, 1985 also clearly seen approximately same trend.

For the waters southwest of Oahu island, the histogram of mantle length (a) and body weight (b) of female and male in November, 1983 are shown in Figs. 7 (a) and (b), and Figs. 8 (a) and (b), respectively.

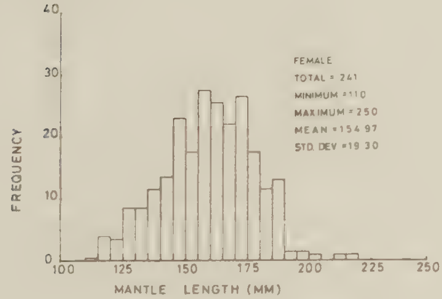

Fig. 3(a). Mantle length composition of *S. oualaniensis* female sampled in waters south of Oahu island in February, 1982.

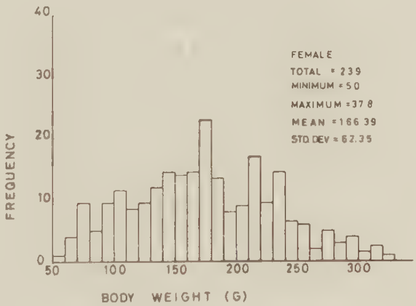

Fig. 3(b). Body Weight composition of *S. oualaniensis* female sampled in waters south of Oahu island in February, 1982.

male, mean mantle length, mean body weigth, and maturity of each year

Female					Male				
Mean ML (mm)	Mean BW (g)	Maturity %			Mean ML (mm)	Mean BW (g)	Maturity %		
		1	2	3			1	2	3
155.0	166.6	96	0	4	139.4	120.4	9	8	82
164.7	223.6	87.5	0	12.5	147.8	141.5	0	0	100
164.2	215.1	71.8	14.1	14.1	140.1	123.1	7.5	12.5	67.5
191.3	390.1	48.7	6.9	44.4	142.6	123.4	27	17	56.0
143.2	122.4	99.9	0	0.03	137.8	105.5	78.6	5.8	15.6
206.6	419.2	—	—	—	149.4	150.7	—	—	—

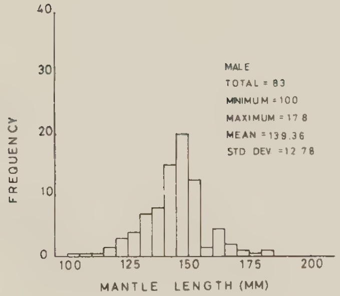

Fig. 4(a). Mantle length composition of *S. oualaniensis* male sampled in waters south of Oahu island in February, 1982.

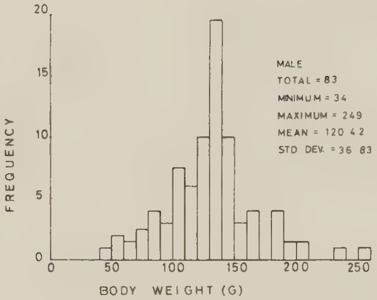

Fig. 4(b). Body weight composition of *S. oualaniensis* male sampled in waters south of Oahu island in February, 1982.

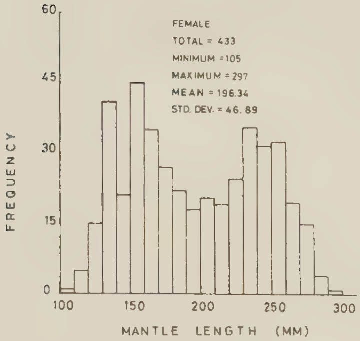

Fig. 5(a). Mantle length composition of *S. oualaniensis* female sampled in waters east of Hawaii island in February, 1983.

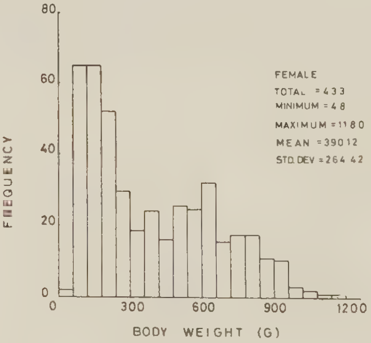

Fig. 5(b). Body weight composition of *S. oualanienis* female sampled in waters east of Hawaii island in February, 1983.

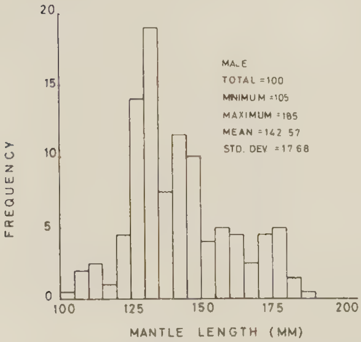

Fig. 6(a). Mantle length composition of *S. oualaniensis* male sampled in waters east of Hawaii island in February, 1983.

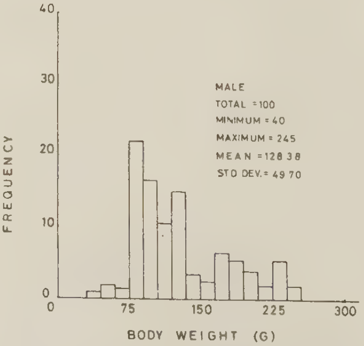

Fig. 6(b). Body weight composition of *S. oualaniensis* male sampled in waters east of Hawaii island in February, 1983.

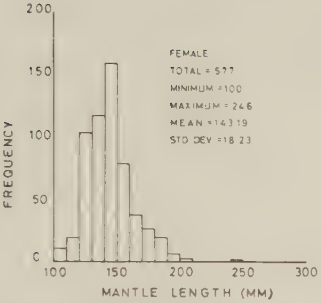

Fig. 7(a). Mantle length composition of *S. oualaniensis* female sampled in waters southwest of Oahu island in November, 1983.

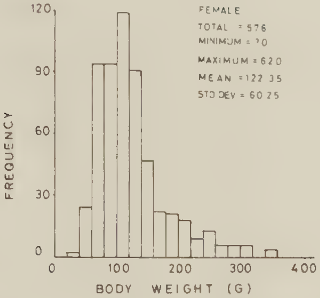

Fig. 7(b). Body weight composition of *S. oualaniensis* female sampled in waters southwest of Oahu island in November, 1983.

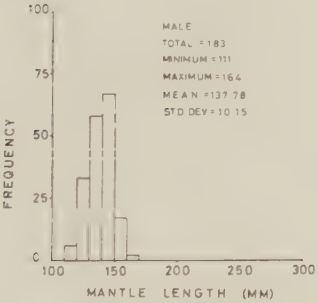

Fig. 8(a). Mantle length composition of *S. oualaniensis* male sampled in waters southwest of Oahu island in November, 1983.

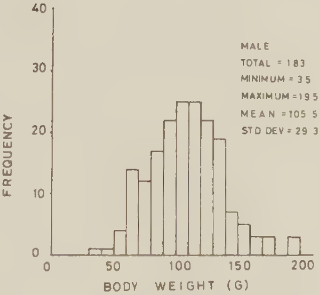

Fig. 8(b). Body weight composotion of *S. oualaniensis* male sampled in waters southwest of Oahu island in November, 1983.

Table 4 Mean CPUE and its confidence intervals of catch year

Year	1981, Feb.	1982, Feb.	1983, Feb.	1983, Feb.	1983, Nov.	1985, Feb.
Fishing Ground	Oahu Is. South	Oahu Is. South SW	Oahu Is. South	Hawaii Is. East	Oahu Is. Southwest	Hawaii Is. East
CPUE	1.43 (0-4.7)	0.5 (0.1-1.2)	0.7 (0.06-1.2)	6.2 (2.9-9.7)	7.6 (3.8-13.3)	2.70 (0.33-6.0)

Results of fitting the mantle length (Y)-body weight (X) relationship of female (1983-1985 years sample) was $Y=0.000018\times^{3.15}$, $r^2=0.9597$ (Fig. 9). Fig. 10 described the mantle length-body weight relationship of male, $Y=0.000042\times^{2.99}$, $r^2=0.7006$.

Further, the water temperature of Hawaiian waters in this season can be

Table 5 Catch of *S. oualaniensis* in off Hilo and southeastern area weight and maturity.

Year	Area	Female-male ratio (%)	Female	
			Mean ML (mm)	Mean BW (g)
1983. Feb	off Hilo	87.5 : 12.2	225.9	548.2
1985. Feb	〃	85.9 : 14.1	228.5	514.74
1983. Feb	Hawaii Is. Southeast	77.4 : 22.6	159.2	190.1
1985. Feb	〃	80.4 : 19.6	136.0	212.4

⁑ Maturity 1 is immature stage, maturity 3 is matured stage.

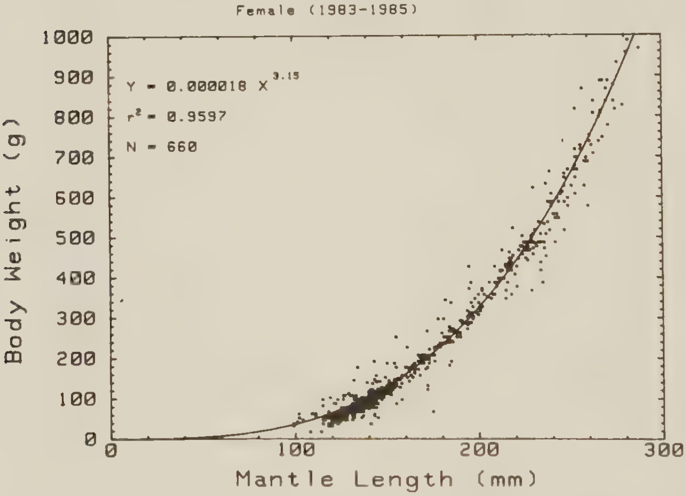

Fig. 9. The relationship between mantle length and body weight of *S. oualaniensis* female.

summarized as follows. The isothermal layer of 24℃ ~25℃ formed until depth 100 m, deeper than this circumstances, water temperature achieving 5℃ for depth 500-600 m. Other than this depth until adjacent 1000 m formed isothermal layer of about 5℃ again.[1)2)]

Discussion

Very few *S. oualaniensis* were distributed in waters south and southwest of Oahu island in February, 1981, 1982 and 1983, indicated by mean CPUE value of 1.4, 0.5, and 0.7 respectively (Table 4). The mean mantle length 140 mm and body weight 130 g of male illustrated almost matured stage (Table 3). On the other hand, 80-90% of female were immature stage (among these, 80-90% have not mate). Moreover, the mean mantle length 160 mm and body weight 200 g of female indicatof Hawaii island and respective mean mantle length, mean body

			Male					
Maturity %			Mean ML (mm)	Mean BW (g)	Maturity %			CPUE
1	2	3			1	2	3	
16.4	6.5	76.8	147.7	140.6	26.7	13.3	60.0	27.2
—	—	—	156.1	156.1	—	—	—	16.5
90.6	5.2	4.2	141.3	126.2	17.9	14.3	69.7	10.7
—	—	—	138.1	130.2	—	—	—	8.9

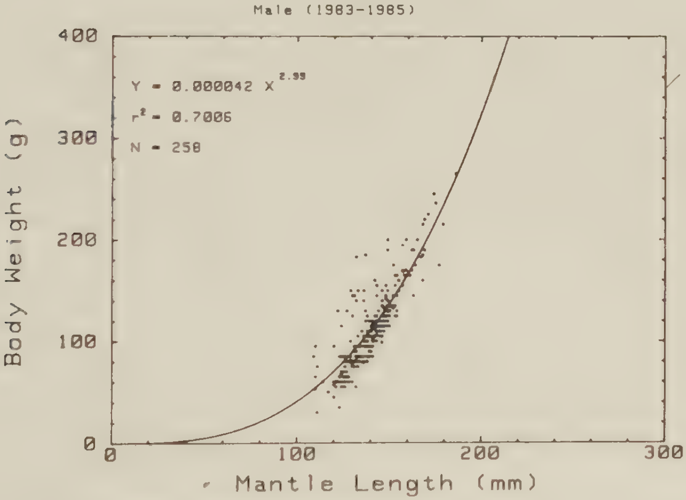

Fig. 10. The relationship between mantle length and body weight of *S. oualaniensis* male.

ed *S. oualaniensis* like other species of squid was male prior maturity and male size smaller than female.

The highest mean CPUE of 7.6 (Table 4) showed high density of *S. oualaniesis* population distributed in southwestern area of Oahu island in November compared to February results. About 80% of male which having mean mantle length of 138 mm and body weight of 105 g was immature stage; and 99.9% of female with 143 mm mean mantle length and 122 g mean body weight was immature. This suggests that the small size of both male and femle may be immature stage.

As shown in Table 4, in February, 1983 and 1985, a very high density (mean CPUE of 6.2 and 2.7 respectively) of *S. oualaniesis* population distributed in waters east of Hawaii island compared to the same season in southern area of Oahu island

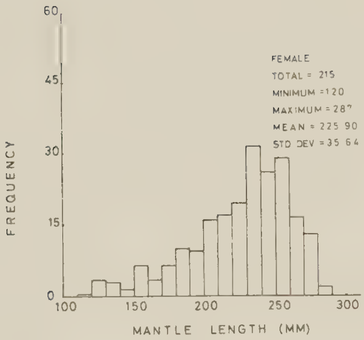

Fig. 11(a). Mantle length composition of *S. oualaniensis* female in waters off Hilo of Hawaii island in February, 1983.

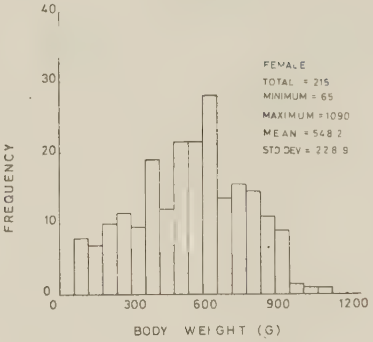

Fig. 11(b). Body weight composition of *S. oualaniensis* female in waters off Hilo of Hawaii island in February, 1983.

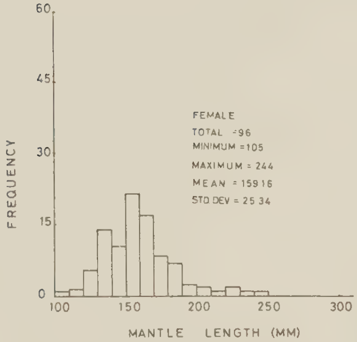

Fig. 12(a). Mantle length composition of *S. oualanienis* female in waters of southeast of Hawaii island in February, 1983.

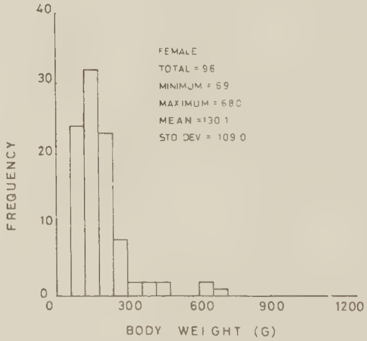

Fig. 12(b). Body weight composition of *S. oualaniensis* female in waters of southeast of Hawaii island in February, 1983.

as described above. The mantle length and body weight of male has almost same as another area. But the female has mean mantle length of about 200 mm and mean body weight of about 450 g, which is a very large size. The degree of maturity also high, about 50% was fully in matured condition (in 1985 season only mantle length and body weight were measured).

Because of clearly seen the different size of female body, in the east of Hawaii island, the central off Hilo of Hwaii island (St. HOAJ 8301-8303, St. HOAJ 8526, 28, 29, 30, 32 in Fig. 1) and waters southeast of Hawaii island (St. HOAJ 8308-8310, St. HOAJ 8505, 17-20 in Fig. 1), these data was rearranged.

The mantle length and body weight of off Hilo and southeast off of Hawaii island given in Fig. 11 and Fig. 12, respectively. Table 5 shows the respective mean mantle length, mean body weight and maturity obtained off Hilo and waters southeast of Hawaii island. Based on these data, the population of off Hilo was large size matured, and immature for waters southeast of Hawaii island. The CFUE of off Hilo also indicated by large size matured female stage was concentrated in this area.

Figs. 9 and 10 show the mantle length-body weight relationship of female and male, respectively. The mean mantle length of female of off Hilo in November achieving 143 mm, three months later in February this mantle length was 225 mm. It is considered that this mean mantle length composition suggests the mean growth rate. Besides, based on the results as shown in Figs. 9 and 10, and maturity stage in Table 3 and 5, it is conjectured that flying squid has same life cycle with other squid species of family Ommastrephidae.

From the results that matured stage was concentrated in off Hilo, this area was considered as one of the spawning ground. Spawned in off Hilo, during floating period after hatching, they transfered to westward by northern equatorial current from Oahu island to surrounding Hawaii islland. The swimming capability increased with growth and then they migrate to east ward reaching surrounding Oahu island again, from October to December become distributed as immature stage. Eventually they reach to spawning grounnd of off Hilo of Hawaii island, during a period from January to March. This pattern was considered as the life cycle of *S. oualaniensis* in Hawaiian waters (Fig 13). In November the high abundant immature stage was distributed in waters southwest of Oahu island, and low abundant distributed three months later (in February). This supports our hypothesis.

Also from the previous report[3], it was described that flying squid *S. oualaniensis* distributed in illimitable areas, from Indian ocean to the center part of Pacific ocean and exist subpopulations. So it is considered that the subpopulation of *S. oualaniensis* which can distributed in waters adjacent Hawaii islands. The spawn-

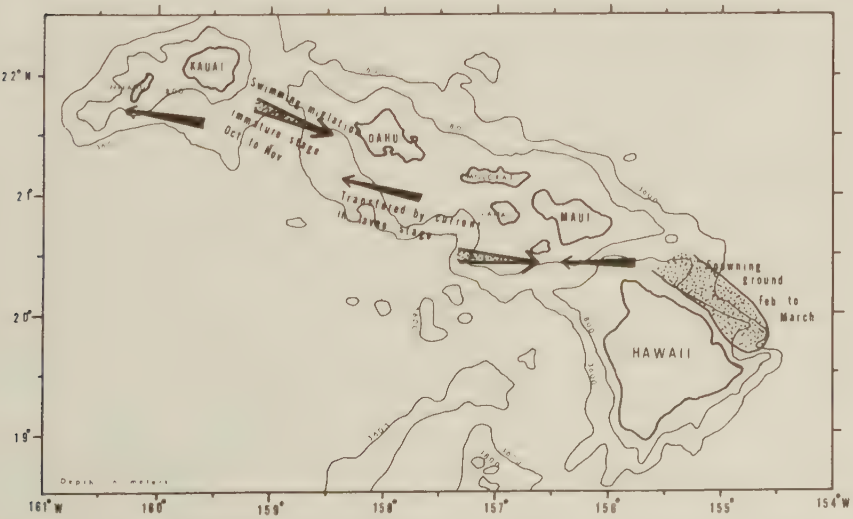

Fig. 13. Schematic representation of the life cycle period of *S. oualaniensis* in Hawaiian waters in February to March spawning population (Hypothesis).

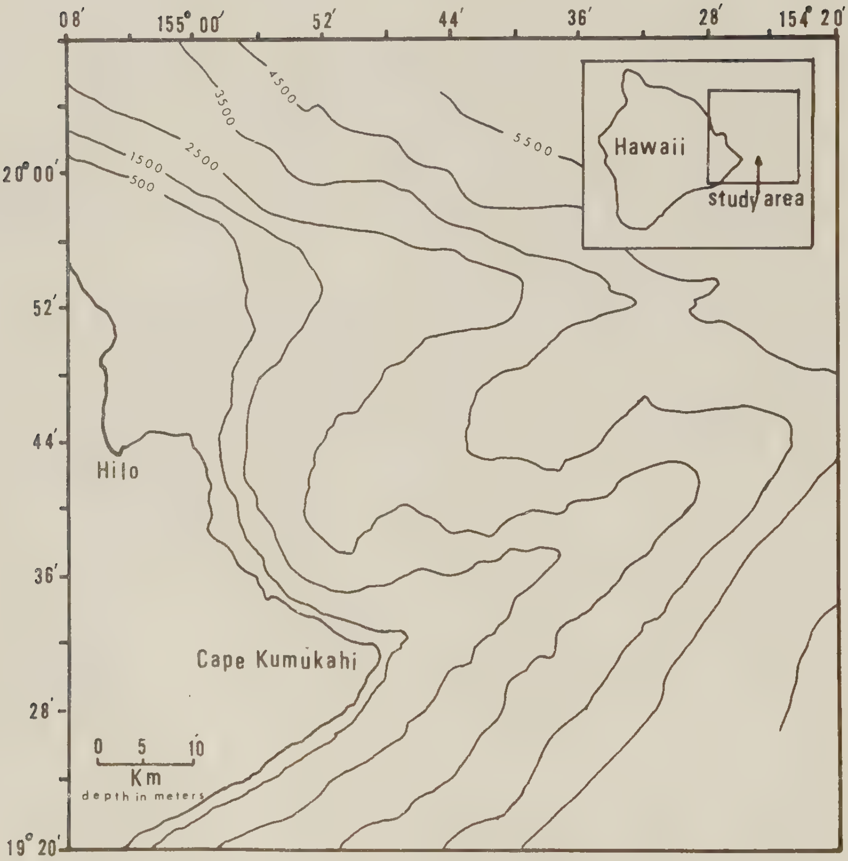
08'
155° 00'
52'
44'
36'
28'
154° 20'
20° 00'
52'
44'
36'
28'
19° 20'
4500
3500
5500
2500
1500
500
Hawaii
study area
Hilo
Cape Kumukahi
0 5 10
Km
depth in meters

Fig. 14. Depth contours off Hilo of Hawaii island.

ing ground of this subpopulation was considerd in off Hilo. Hereafter, to gather more detail information, continued research is very important.

Why off Hilo was considerd as one spawning ground, the reasons investigated[4] consist of nutrient salts, plankton distribution, water temperature, and salinisy. At present time, the particular cause could not be founded. Fig. 14 shows the depth contours of off Hilo, Hawaii island. At the southern Hilo, it has outlet of sea trench, depth of this part of ridge shallower than surrounding parts. The topography of this ara could be significant to understand why this area could be a spawning ground by *S. oualaniensis* and must be studied carefully in future.

Other hand Hilo fisherman[5] reports that many matured stage *S. oualaniensis* gathered at off Hilo same area in August. This fact is suggested to exist another subpopulation of *S. oualaniensis* in Hawaiian waters, but we have not any informations in this matter. So necessary to research other seasons in future.

Acknowledgements

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STARVATION-INDUCED MORTALITY OF YOUNG SEA-CAUGHT JACK MACKEREL, *TRACHURUS SYMMETRICUS*, DETERMINED WITH HISTOLOGICAL AND MORPHOLOGICAL METHODS

GAIL H. THEILACKER[1]

ABSTRACT

Young jack mackerel, *Trachurus symmetricus*, living offshore are starving while those living nearshore are healthy. These results for sea-caught jack mackerel were determined by using histological and morphological criteria that reliably diagnosed the viability of laboratory-raised jack mackerel. Both the histological and morphological indices indicated that 350 km offshore about 70% of the first-feeding jack mackerel were starving. In contrast, 12% of the fish collected near islands and banks were starving. In both habitats, mortality rates decreased to zero for jack mackerel at 2 weeks of age. The accuracy of the techniques for prediction of the nutritional state of wild larvae is discussed and evaluated.

Jack mackerel, *Trachurus symmetricus*, hatch with yolk reserves that last for 5 d at 15°-15.5°C. After the yolk is absorbed, they must eat within 3 d or die of starvation. In addition, growth is retarded in larvae that have experienced only 1 d of starvation, and resumption of normal growth does not occur until 2-3 d after the starvation period (Theilacker 1978, 1981). Thus, in the laboratory, availability of food at the time of first feeding affects growth and survival of young jack mackerel. In the field, the relative importance of starvation as a source of mortality of jack mackerel is unknown. It was first suggested by Hjort (1914) (reviewed by May 1974) that the strength of the year class is determined early in life by the availability of food for larvae at the time of first feeding (the critical period hypothesis). But only recently (O'Connell 1980) has the presence of starving ocean-caught larvae been documented. In this study I give evidence that starvation may be a major cause of natural mortality of young jack mackerel at sea. I use two techniques, developed in the laboratory, to determine the incidence of starvation (Theilacker 1978). The potential use of these techniques to monitor sea samples for larval survival is discussed.

METHODS

Collection

In May 1980 a concentration of jack mackerel eggs and larvae was located 350 km off the coast of California (lat. 31°00′N and long. 120°30′W). A 400 mi^2 grid was established which contained 41 stations, 4 mi apart; it took 4 d to sample all stations (Fig. 1). At each station, a standard oblique bongo net tow (Smith and Richardson 1977) and a 1 m net sample were taken. The bongo samples will be used in another study to estimate growth and mortality of jack mackerel larvae (Hewitt et al. in press). The 1 m net (505 μm mesh) was used to sample larvae qualitatively from the upper 50 m of water. Ahlstrom (1959) found that 88% of the larval jack mackerel collected off California were in the upper 50 m, and all the jack mackerel collected by Devonald (1983) were above 42 m. A special collection procedure was used for the samples taken for histological and morphological analyses. Immediately after the net tow, the sample was preserved in Bouin's solution to avoid autolysis of larval tissues (elapsed time was usually 8 min) (Theilacker 1978). The collecting net was not washed down (a procedure required for quantitative samples), and the cod end containing the sample was placed directly into Bouin's solution. The preserved sample was removed from the cod end within an hour. After 2 d, Bouin's solution was replaced by 70% alcohol.

In addition to jack mackerel collections taken in the open ocean 350 km offshore, a few special tows (n = 24) for assessment of starvation were made during routine cruises in 1978, 1979, and 1980 near the Channel Islands (Anacapa, Santa Barbara, and San Clemente) and Tanner Bank.

Preparation of Fish

More than 2,000 jack mackerel were collected in

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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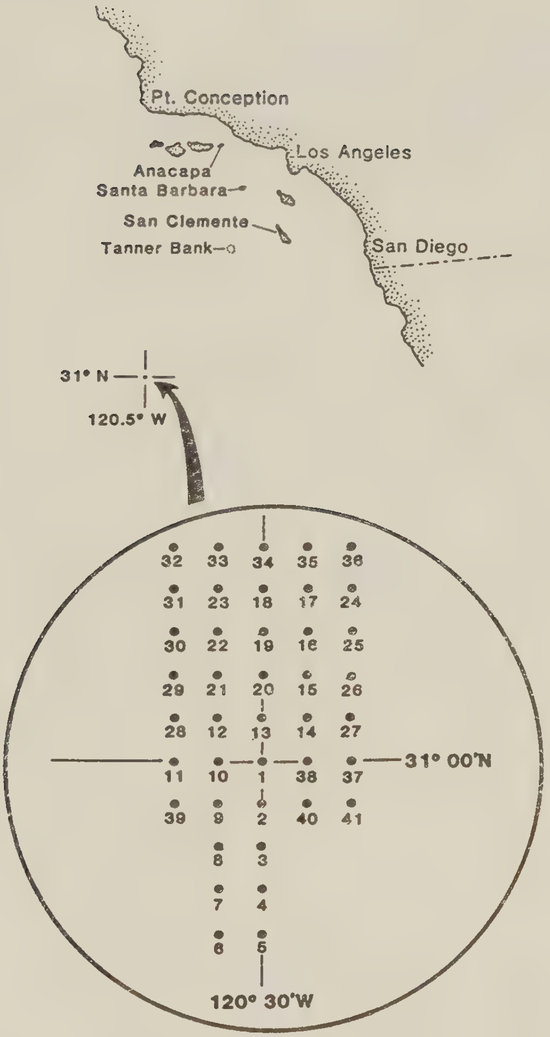

FIGURE 1.—Location of jack mackerel, *Trachurus symmetricus*, collections off the coast of California. Nearshore stations were at Anacapa, Santa Barbara, and San Clemente Islands and at Tanner Bank. The grid of open-ocean stations was 350 km offshore; stations were 4 mi apart.

samples taken offshore; from 0 to 262 fish were caught per sample (Table 1). Larvae sorted from the samples (n = 445) were counted and five body measurements taken: standard length (SL, tip of upper jaw to perpendicular at end of notochord); head length (HL, tip of upper jaw to cleithrum); eye diameter (ED); body depth at the pectoral (BD-1); and body depth at the anus (BD-2). After measurement, some larvae (n = 369) were prepared for histological examination. When samples contained fewer than 50 jack mackerel, most larvae were examined, but when samples contained more than 100 jack mackerel, about 25% of the fish were examined histologically. Jack mackerel size distribution in the offshore study area (determined for 400 fish taken from stations 16, 23, 34, and 35) was similar among stations and ranged between 2.6 and 4.7 mm SL. To ensure analysis of all ages in the larger samples, fish were taken equally from each of four length classes: <3.0; 3.0–<3.5; 3.5–<4.0; 4.0–<5.0 mm. These larvae were imbedded in paraffin, sectioned at 6 μm, and stained with Harris hematoxylin and eosinphloxine B (Theilacker 1978). In my analysis of histological data I combined the first two size classes because the size at first feeding was 3.2 mm.

The prevalence of starvation was assessed for 371 jack mackerel selected from 20 of the 32 positive stations (Table 1). In addition, I analyzed 41 jack mackerel taken in 14 hauls from the inshore stations near the Channel Islands and Tanner Bank.

Histological Analysis

The histological assessment of nutritional state is based on distinct cellular changes that occur in tissues when larval jack mackerel were deprived of food; these changes are well documented by Umeda and Ochiai (1975), O'Connell (1976), and Theilacker (1978). To determine the condition of individual ocean-caught jack mackerel, I used the histological criteria I developed in the laboratory by starving jack mackerel except I did not grade the pancreas. Grades were assigned to 11 histological characteristics of the brain, digestive tract, liver, and musculature (Theilacker 1978, 1981). Fish identities were unknown during this examination. I classified jack mackerel larvae into four categories (healthy, recovering, starving, and dying) according to their histological scores (the summation of the grades for each of the 11 histological characteristics).

Tissues of jack mackerel from the sea which had tissues similar in appearance to the tissues of feeding, laboratory-raised fish were classified as healthy; sea-caught jack mackerel which resembled laboratory fish that had fasted before eating were classified as recovering (these fish showed signs of feeding and digestion, but also showed signs of starvation); sea-caught larvae which were classified as starving resembled larvae that had been starved in the laboratory for 1-3 d (Theilacker 1978, 1981). I did not observe the dying category in laboratory-starved larvae; this category is described in Results.

Morphological Analysis

To detect starvation I used a set of morphological

TABLE 1.—Number of jack mackerel collected and the condition of those that were analyzed histologically.

Station No.	Number of fish					
	Sampled	Analyzed	Dying	Starving	Recovering	Healthy
Offshore						
1	0	0				
2	2	1	0	0	1	0
3	0	0				
4	2	0				
5	0	0				
6	0	0				
7	2	1	0	1	0	0
8	2	2	0	0	2	0
9	1	1	1	0	0	0
10	0	0				
11	3	3	3	0	0	0
12	0	0				
13	1	0				
14	1	0				
15	>200	0				
16	>200	0				
17	20	13	0	8	5	0
18	>125	0				
19	43	35	7	0	1	27
20	242	64	8	19	13	24
21	>250	0				
22	>175	0				
23	150	32	1	0	4	27
24	1	0				
25	23	0				
26	4	3	3	0	0	0
27	0	0				
28	262	58	3	36	14	5
29	11	11	1	4	4	2
30	250	57	4	13	18	22
31	32	9	7	1	0	1
32	109	25	0	2	20	3
33	31	23	1	3	10	9
34	38	0				
35	43	0				
36	31	24	3	4	1	16
37	7	5	2	1	2	0
38	2	2	1	0	0	1
39	0	0				
40	1	0				
41	0	0				
Total (Offshore)	>2,264	369	45	92	95	137
Around Islands						
Anacapa	12	12	0	1	0	11
Santa Barbara	3	3	0	0	2	1
San Clemente	17	17	0	1	5	11
Tanner Bank	9	9	0	1	0	8
Total (Nearshore)	41	41	0	3	7	31

characteristics that successfully diagnosed the extent of starvation in 85% of the laboratory-reared jack mackerel (Theilacker 1978). The technique is based on a stepwise discriminant analysis (SWDA) using 11 body part measurements. The analysis allowed me to distinguish between individuals belonging to fed and starved treatments, given a set of morphological measurements that describe the characteristics of the individuals in each feeding treatment. The 11 body part measurements used to distinguish between groups of fed and starved jack mackerel were 1) head length, 2) eye diameter, 3) body depth at the pectoral, 4) body depth at the anus, 5) head length/standard length, 6) eye diameter/standard length, 7) body depth at the pectoral/standard length, 8) body depth at the anus/standard length, 9) eye diameter/head length, 10) body depth at pectoral/head length, and 11) body depth at anus/head length. Standard length was used in the ratios but not as a unit to allow discrimination between feeding and starving fish of the same length.

Adjustment for Shrinkage

In order to use morphological measurements to diagnose starvation of jack mackerel, it is essential to adjust for shrinkage of body measurements. Both handling and preservation cause shrinkage of larval fishes, and the amount of shrinkage varies among body parts. Final fish size is dependent not only on initial size but also on the handling time (which is different for the laboratory and the field) and the type of preservative used (Blaxter 1971; Theilacker 1980a; Hay 1981). The shrinkage of laboratory specimens of jack mackerel preserved in Bouin's solution is known (Theilacker 1980a), but for field-collected specimens the shrinkage caused by the net tow and the subsequent effect of Bouin's preservative must be evaluated.

I conducted laboratory experiments to estimate the amount of shrinkage caused by handling (net retention) and by preservation. Live jack mackerel were pipetted individually (time = 0) onto a slide, and four body measurements were taken before placing the fish into a net container through which 15°C seawater circulated. Standard length, head length, eye diameter, and body depth at the anus were measured. Body depth at the pectoral fin was not measured because it was difficult to measure quickly on live jack mackerel. During net treatments, I usually remeasured each fish four more times at 5-7 min intervals, replacing the fish in the net between each set of measurements. After 25-30 min, the fish were preserved in either Bouin's fixative (used for histological analyses) or 5% buffered Formalin[2] (as per shipboard procedures; Smith and Richardson 1977). Remeasurements after preservation were taken in 3-4 wk.

Shrinkage of net-captured larval fish has been shown to decrease with increasing fish size. For example, shrinkage of northern anchovy decreased from 19% at 4 mm SL to 8% at 18 mm SL (Theilacker 1980a). The jack mackerel tested in this study ranged between 3.35 and 4.10 mm SL, and within this restricted length group shrinkage was proportional to size. Thus for the shrinkage analyses, all jack mackerel were combined into one group.

For the combined size group, length of the jack mackerel body (Fig. 2) and the head continued to shrink for the duration of the net treatment. Width of the body (Fig. 3) and the eye shrank initially, and then remained relatively constant during additional treatment. To account for positive correlation between body parts, a multivariate analysis (Table 2) was used to relate the ratio of net-treated size to live size (for each body part) with treatment time. Individual shrinkage was highly variable; for example, shrinkage of body depth varied between 0 and 23% for treatment times between 5 and 20 min (Fig. 3). However, since these were the best estimates of average shrinkage for body parts, the regressions (Table 2) were used to calculate the adjustment factors needed for this study. Factors for each body part

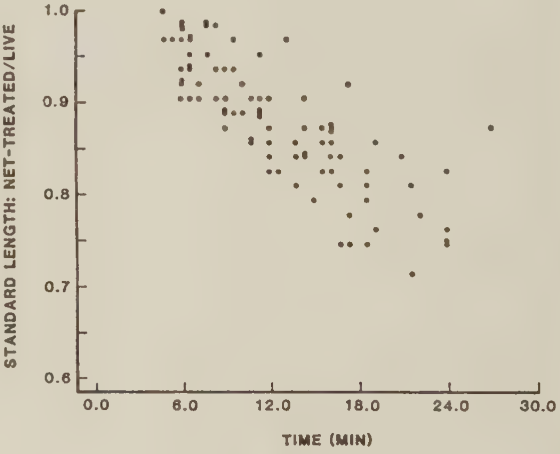

FIGURE 2.—Shrinkage of standard length, shown as the ratio of net-treated size to live size, of individual *Trachurus symmetricus* larvae as a function of net-treatment time; estimated parameters are in Table 4.

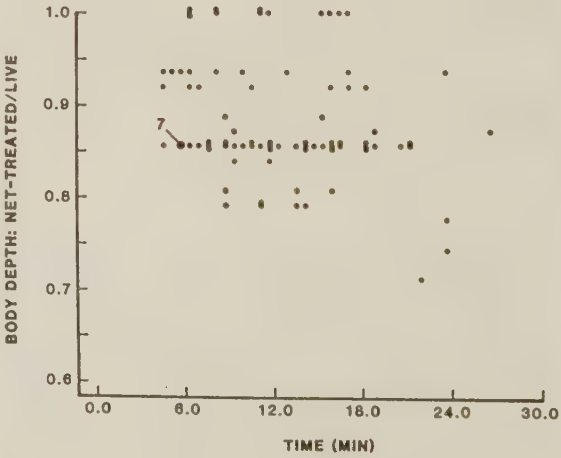

FIGURE 3.—Shrinkage of body depth, shown as the ratio of net-treated size to live size, of individual *Trachurus symmetricus* larvae as a function of net-treatment time; estimated parameters are in Table 4.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Shrinkage of jack mackerel larvae. Parameters estimated from multivariate linear equations relating the ratio of the net-treated size of a mackerel body part to its live size (y) with the net-treatment time (x).

Net-treated size/ live size[1]	a	(SE)	b	(SE)	P[2]	r^2
Standard length (SL)	1.0109	(0.0117)	−0.0105	(0.0008)	<0.001	0.66
Head length (HL)	0.9281	(0.0157)	−0.0038	(0.0011)	0.001	0.12
Eye diameter (ED)	0.9360	(0.0168)	−0.0027	(0.0012)	0.031	0.06
Body depth (BD-2)	0.8980	(0.0177)	−0.0014	(0.0013)	0.280	0.02

[1] n = 89.

[2] Probability that slopes differ from zero.

were calculated by 1) combining the shrinkage ratio at 8 min (average elapsed time for field collections, see Methods) with 2) the average shrinkage in Bouin's preservative after the net treatment, and 3) comparing the combined shrinkage with results from shrinkage determined in the laboratory study (Theilacker 1980a; Table 3). Also given in Table 3 are average shrinkage ratios calculated for specified time intervals.

Adjustment factors for standard length, head length, and eye diameter (Table 3) support the view that shrinkage of field-collected fishes is greater than shrinkage of fishes preserved in the laboratory. Shrinkage of BD-2 was an exception to this pattern, however, as less shrinkage occurred under simulated field conditions (20-23%) than in the laboratory (25%). I (Theilacker 1980a) reported a similar paradox for northern anchovy where simulated-field net treatments caused 8% shrinkage of BD-2 as compared with 10% shrinkage for standard laboratory preservation. Jack mackerel shrinkage was greater in Bouin's solution than in Formalin, results which are consistent with studies on northern anchovy. Also, as with northern anchovy, Formalin preservation caused a slight increase in the size of the jack mackerel eye (Table 3).

I adjusted the body measurements of the ocean-caught jack mackerel with the shrinkage factors (ratio R_8, Table 3). Use of these adjustments should equate the morphology of preserved, ocean-caught jack mackerel (this study) with the morphology of preserved, laboratory-raised jack mackerel that were used to develop the morphological SWDA (see Methods: Morphological Analysis). It was necessary to reestimate the SWDA function for this study, although nearly the same analysis was made previously (Theilacker 1978). A new estimate was required because pectoral body depth was not included in the shrinkage measurements in this study; hence, an SWDA function that excluded this measurement was needed. Elimination of pectoral body depth from the analysis reduced the level of predictability from 85% to 78%. This new function was used here to classify the condition of ocean-caught jack mackerel

TABLE 3.—Shrinkage of jack mackerel larvae[1]. Treatment ratio (R) is treated size divided by previous size (1.00 = no shrinkage).

Treatment ratio	R	n	Mean time	Ratios: Standard length	Head length	Eye diameter	Body depth
8 min net/live size	[2]R_1	89	8	0.93	0.90	0.91	0.89
5-10 min net/live size	R_2	36	7.3	0.94	0.90	0.92	0.89
11-15 min net/live size	R_3	22	12.6	0.87	0.88	0.88	0.86
16-28 min net/live size	R_4	27	19.4	0.81	0.86	0.89	0.88
Bouin's fixative/ net-treated size	[3]R_5	15	—	0.91	0.84	0.93	0.91
Formalin fixative/ net-treated size	[3]R_6	13	—	0.96	0.93	1.08	0.91
Laboratory-preserved in Bouin's fixative live size	[4]R_7	45	—	0.92	0.82	0.90	0.75
Calibration factor = $R_7/R_1 \times R_5$	[5]R_8	—	—	1.09	1.08	1.06	0.93

[1] Range in standard length 3.35-4.10 mm.

[2] Calculated from regression (Table 2); ocean-caught fish preserved within 8 min; see text.

[3] Shrinkage in fixative after net treatment.

[4] Data from Theilacker (1980a).

[5] Adjustment factor to equate measurements of field-collected mackerel (this study) with measurements of laboratory-raised mackerel (Theilacker 1978).

after the size of their body parts was adjusted for shrinkage.

RESULTS

Habitat Conditions

A larval-density gradient was apparent in the open ocean study area. High densities of jack mackerel larvae (100-<300/sample) were found in the central stations and in stations near the western boundary of the grid; lower densities (20-50) were found to the north and east, and densities of larvae approached zero at the southern stations that were occupied at the beginning and again at the end of the 4-d observation period (Fig. 4). Larval densities in the south did not change during this period.

The study area was chosen because temperature, viewed on satellite thermal image of the sea surface, corresponded to the temperature range (15°-16°C) associated with jack mackerel spawning (Farris 1961). Surface temperature in the study area increased from 15.2°C in the north to 16.8°C at the southern stations, with the majority of jack mackerel found in water temperatures of 16.1°-16.6°C. Water temperatures inshore of the grid were about 14°C.

A temperature-salinity curve obtained at station 19 (Fig. 1) agreed well with the curves obtained from inshore stations with the exception of the warm-water portion of the curve, which appeared to be a thin, warm lens of open ocean water intruding coastward over deeper coastal water.

Histological Assessment of Fish Condition

I used the tissue characteristics of laboratory fish (raised at 15.0°-15.5°C) of known feeding history as the criteria to determine the nutritional condition of the sea-caught jack mackerel. Photomicrographs of the diagnostic tissue characteristics were documented by Theilacker (1978). Many of these characteristics are shown also for wild fish (Fig. 5, see also Figures 6-14). In addition, the wild fish exhibited four tissue conditions that were not observed in the laboratory: lesions in the brain; luminal vacuoles in the midgut; total degeneration of the midgut mucosal cells; and a wavy configuration of the muscle fibers. Each of these conditions will be considered in the following section that describes the tissues of ocean-caught fish. My emphasis will be on those tissue characteristics that diagnose starvation in young jack mackerel.

Brain

The brain of an ocean-caught jack mackerel was considered normal when the neurons were distinct, round, and closely spaced. In these fish, brain cell division was common, but it was not graded. One percent of the jack mackerel examined had brain lesions of the type (Fig. 6) induced by ultraviolet light in larval northern anchovy, *Engraulis mordax*, and Pacific mackerel, *Scomber japonicus* (Hunter et al. 1979). The grading system classified these jack mackerel ($n = 3$) into the healthy category. In a

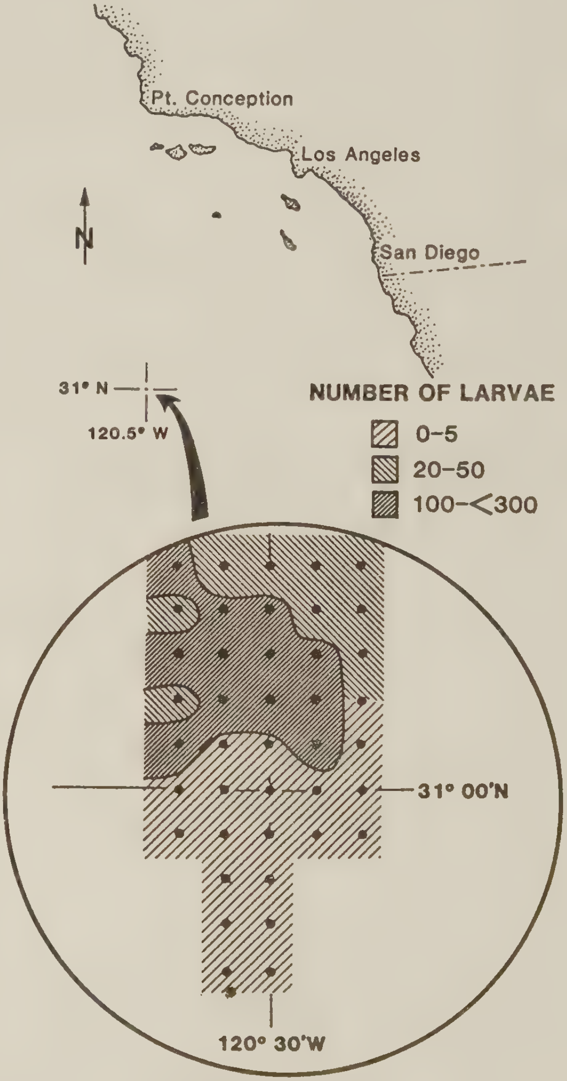


FIGURE 4.–*Trachurus symmetricus* larval density gradient shown as number of larvae collected per sample (not quantitative). Station grid located 350 km off the coast of California.

single specimen, lesions were present not only in the brain but throughout the spinal cord (Fig. 7) as well. In addition, the gut and associated glands had deteriorated to the extent that this fish was considered starving.

An abnormal central nervous system of a jack mackerel larva consisted of vacuolar degeneration and shrinkage of neurons. The degenerating neurons exhibited increased staining (Fig. 8).

Digestive Track and Associated Glands

The midgut mucosa of young jack mackerel is composed of a single layer of columnar epithelial cells. Older fish (3.7-4.0 mm) showed increased mitotic activity in the basal layer. Microvilli bordered the midgut lumen only in fish that appeared healthy. Mucosal cells were closely united in the fish considered to be normal (Figs. 9, 10). Basal separations between these cells were common, not only in fish that appeared to be starving but also in fish that showed signs of feeding and digestion (Fig. 11). O'Connell (1980) also reported that sea-caught northern anchovy exhibited basal separations between mucosal cells while the apical portions were well joined.

All wild jack mackerel categorized as recovering had basal separations between midgut mucosal cells. Laboratory fish that were artificially starved for 1-2 d before feeding showed these separations for several days after feeding resumed. In the laboratory, larvae did not grow while their tissues were regenerating (Theilacker 1981).

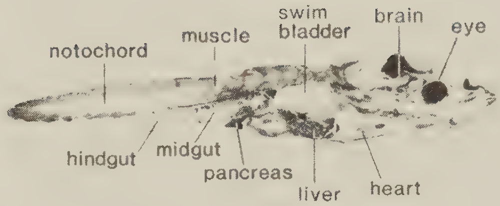
Many sea-caught jack mackerel of all ages had intracytoplasmic vacuoles in the midgut epithelium. Basal and membrane lined, these vacuoles resembled the vacuolar condition found in some recovering, laboratory fish (Theilacker 1981). In addition, many sea-caught larvae had smaller, luminal vacuoles that were found in the laboratory fish (Fig. 12). These luminal vacuoles may indicate a degenerative condition. In higher vertebrates a metabolic imbalance can cause vacuolar degeneration. Vacuolation appears first as numerous small, clear vacuoles dispersed throughout the cytoplasm. As the condition becomes more severe, these minute vacuoles coalesce to form large (sometimes single) clear spaces that displace the nucleus (Anderson 1971). On the other hand, the numerous luminal vacuoles can secrete mucous into the lumen or store fat. Use of a routine mucicarmine staining was negative for the presence of mucous cells. Unfortunately, the presence of fat in the vacuoles could not be tested because fat is removed during tissue preparation by clearing agents. Neither vacuolar condition was graded.

Another unusual condition of the midgut occurred in many of the smaller wild jack mackerel. In these fish, the margin of the lumen had lost its integrity, microvilli were absent, and the sloughing of the mucosal cells into the lumen (a condition common in starved laboratory jack mackerel) appeared to have progressed until the lumen contained masses of undefinable, cellular material (Fig. 13). O'Connell (1980) described a comparable condition which he found in the midgut of a single, northern anchovy specimen, the smallest examined. All jack mackerel exhibiting this condition were smaller than the size attained at first feeding, indicating shrinkage had occurred. The hindgut also contained necrotic debris, and other diagnostic tissues were in poor condition. These jack mackerel were classified as dying.

Hindgut mucosal cells of wild jack mackerel typically showed eosin-staining inclusions that are reported to be sites of intracellular digestion (Iwai 1968, 1969; Iwai and Tanaka 1968; Watanabe 1981). Inclusions in the wild jack mackerel varied in intensity; in healthy specimens the intensity appeared to be related to time of day (feeding period), increasing during daylight hours and decreasing during the night. Although the presence and intensity of hindgut inclusions were noted, they were not graded. Inclusions were not present in larval teleosts deprived of food in the laboratory (Theilacker 1978; Umeda and Ochiai 1975; O'Connell 1976). However, in many wild jack mackerel showing signs of starvation the presence of pale inclusions indicated that the fish had eaten at some time in the past.

The key diagnostic characteristics of the pancreas were obscure in ocean-caught jack mackerel because of the intensity of staining. In laboratory fish, the pancreas was very sensitive to food deprivation. For example, a breakdown in the symmetry of the acinar secretory unit was detectable after 1 d of food deprivation (Theilacker 1978). In the wild fish, the intensity of the staining of the pancreas was difficult to control (see Fig. 12), and I was not able to obtain consistent results, hence the condition of the pancreas was not evaluated.

The jack mackerel liver was considered normal when hepatocytes had clear, distinct nuclei (Fig. 9). The appearance of the cytoplasm was quite variable; in some larvae very few intracellular spaces existed in the cytoplasm of the hepatocytes whereas in others extensive intracellular spaces existed. Presumably these spaces are areas where glycogen and fat are stored within the cell. This presumed incorporation of stores was most marked in healthy


notochord
muscle
swim bladder
brain
eye
hindgut
midgut
pancreas
liver
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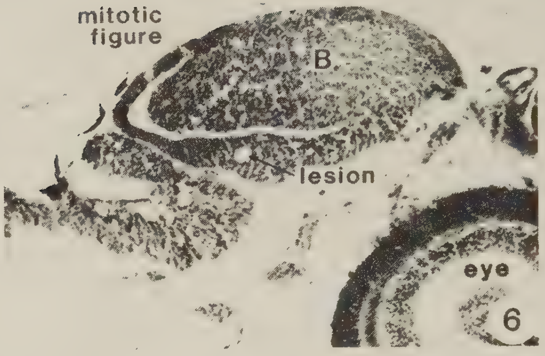
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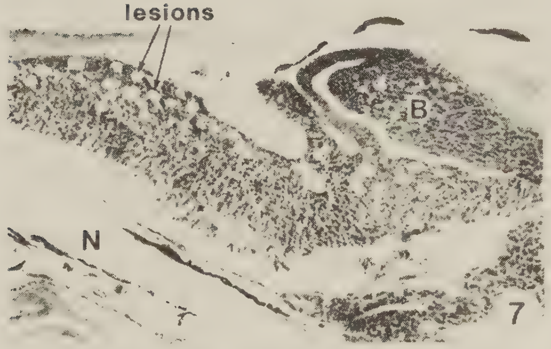
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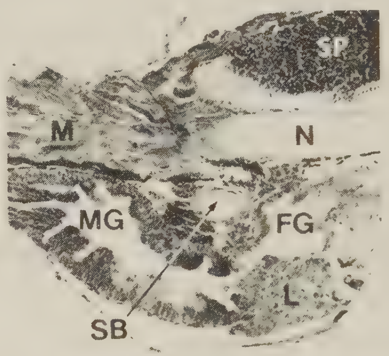
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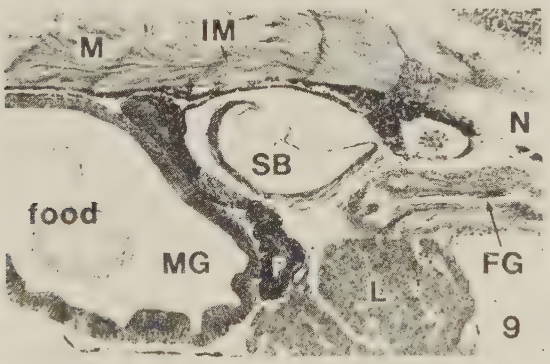
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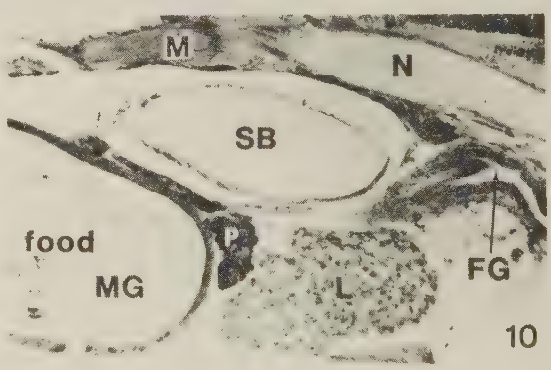
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FIGURE 5.–*Trachurus symmetricus* larva, 3.75 mm SL. All 11 histological criteria graded as healthy. Bar = 281 μm.

FIGURE 6.–Head of *Trachurus symmetricus* larva graded healthy. Mitotic activity and the location of brain lesions are indicated. Bar = 47 μm. B = brain.

FIGURE 7.–*Trachurus symmetricus* larva graded as starving. Lesions present throughout brain and spinal cord. Bar = 47 μm. B = brain, N = notochord.

FIGURE 8.–Pectoral area of a dying *Trachurus symmetricus* larva showing darkly stained primitive nerve cells, wavy muscle fibers, necrotic and atrophied liver, and loss of integrity of midgut mucosal cells. Bar = 47 μm. FG = foregut, L = liver, m = muscle, MG = midgut, N = notochord, SB = swim bladder, SP = spinal cord.

FIGURE 9.–Pectoral area of healthy *Trachurus symmetricus* larva collected offshore showing parallel muscle fibers and abundant intermuscular tissue, distinct nuclei in liver and midgut, and good cellular integrity. Note deflating swim bladder. Bar = 47 μm. FG = foregut, IM = intermuscular tissue, L = liver, M = muscle, MG = midgut, N = notochord, P = pancreas, SB = swim bladder.

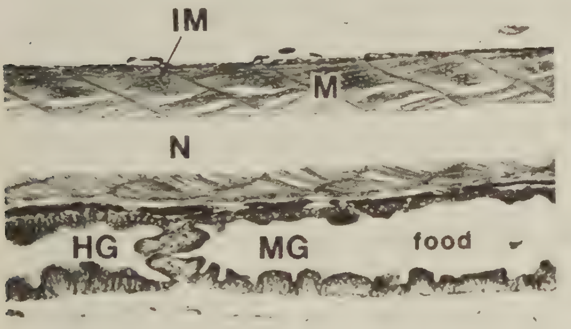
FIGURE 10.–Pectoral area of healthy *Trachurus symmetricus* larva collected near San Clemente Island showing abundant glycogen reserves in the liver. Bar = 47 μm. FG = foregut, L = liver, M = muscle, MG = midgut, N = notochord, P = pancreas, SB = swim bladder.

jack mackerel collected near islands and banks (Fig. 10) whereas healthy jack mackerel collected offshore showed moderate to little storage (Fig. 9).

At the other end of the grading scale, the shrunken livers of jack mackerel considered to be starving contained darkly stained hepatocytes composed of evenly stained cytoplasm with indistinct, irregular nuclei.

Musculature

Healthy muscle tissue in jack mackerel had the following characteristics: few spaces between the muscle fibers; distinct and parallel, striated myofibrils; and abundant, basophilic and nucleated intramuscular tissue (Fig. 9). Nourishment was considered inadequate in fish exhibiting separated (Figs. 11, 14) and hyaline muscle fibers (Fig. 13) and a reduction (Figs. 11, 14) or absence (Fig. 13) of intramuscular tissue. In some sea-caught jack mackerel, muscle fibers were wavy (Fig. 8). Presence of wavy muscle fibers in wild fish was considered abnormal because it was always associated with the poor condition in the other diagnostic tissues, but this characteristic was not used in classification. In starved laboratory fish, nonparallel fibers were reported (Theilacker 1978, 1981), but the wavy pattern was unusual. There were fish with intermediate spaces between muscle fibers that, according to the scores of the other diagnostic tissues, appeared healthy. The



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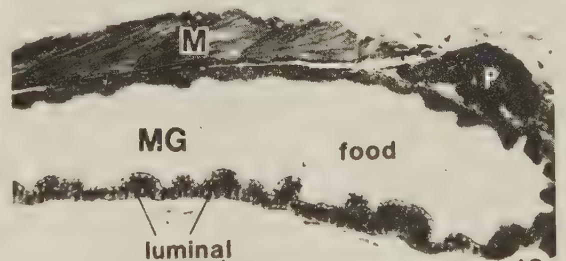

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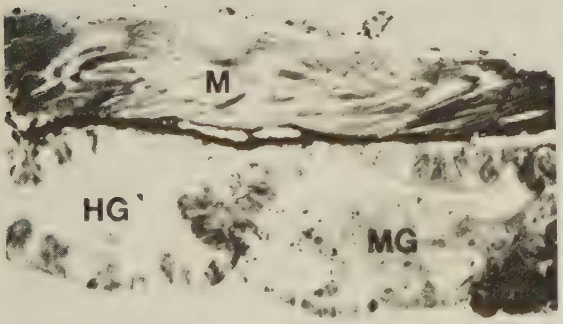

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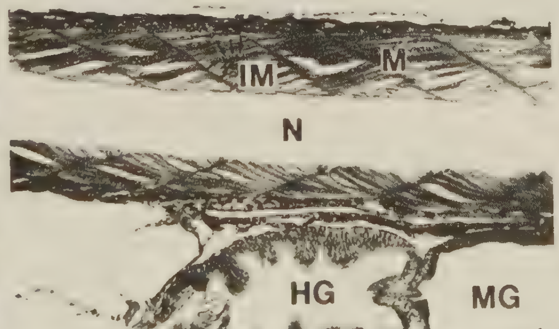

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FIGURE 11.—*Trachurus symmetricus* larva graded recovering. Prominent separations between midgut and hindgut epithelial cells, slight muscle fiber separation and intermediate intermuscular tissue containing distinct nuclei. Bar = 47 μm. HG = hindgut, IM = intermuscular tissue, M = muscle, MG = midgut, N = notochord.

FIGURE 12.—Healthy *Trachurus symmetricus* larva showing luminal vacuoles in the midgut. This histological characteristic was not graded. Bar = 47 μm. M = muscle, MG = midgut.

FIGURE 13.—*Trachurus symmetricus* larva graded dying. No intermuscular tissue; hyaline muscle fibers; total degeneration of midgut mucosa. Bar = 34 μm. HG = hindgut, M = muscle, MG = midgut.

FIGURE 14.—Recovering *Trachurus symmetricus* larva showing slight muscle fiber separation and slight reduction of intermuscular tissue. Bar = 47 μm. HG = hindgut, IM = intermuscular tissue, M = muscle, MG = midgut, N = notochord.

grading system usually classified these fish into the recovering category.

General Histological Observations

In jack mackerel that were considered healthy, swim bladder inflation was first noted at 3.4 mm. Swim bladders were inflated in larvae taken at night whereas they were deflated in those taken in the day. The swim bladders of 72% of the fish were deflated by 0700 (n = 81) except for fish scored in the starving category where inflation was common at any time of day, which was possibly a symptom of starvation or an additional energy-sparing function of the swim bladder (Hunter and Sanchez 1976).

Theilacker (1978) pointed out that the gallbladder was always enlarged in jack mackerel that were deprived of food in the laboratory, and this condition occurred in sea samples of starved larvae taken in the day. On the other hand, gallbladder enlargement was also found in the healthy fish as well as starved fish collected at night. According to Love (1970), the gallbladder discharges its contents when stimulated by food. Jack mackerel do not eat at night, so the gallbladder of healthy fish may remain distended during the night. Thus enlargement of the gallbladder was not used to diagnose starvation. Theilacker's (1978) samples of fed and unfed fish were taken only during the day, when feeding occurs.

Mitotic figures in the brain of jack mackerel occurred in fish collected at all times of day and night. On the other hand, mitosis of mucosal cells in the midgut was restricted to the night. It seems that mucosal cells of northern anchovy also divide late at night, when the digestive tracts are empty (O'Connell 1981).

Evidence for Starvation in the Sea

Results of the histological analysis showed that starvation was a major source of mortality for the smallest jack mackerel larvae (<3.5 mm) as 59% appeared to be dying of starvation, 23% were eating but had fasted previously, and only 19% were classed as healthy. The incidence of starving larvae decreased to 16% in the 3.5-4.0 mm size class and was 3% in the older larvae (Table 4). The numbers of fish used for the histological assessment of starvation was adequate for the smallest (<3.5 mm SL) larval size class (coefficient of variation ranged between 0.09 and 0.15 for the four condition categories), but larger samples would be needed to give a reliable estimate of the fraction starving for the older larvae (>3.5 mm SL) because of the low incidence of starvation.

Despite the fact that jack mackerel abundance decreased from west to east and north to south (Fig. 4), I found no consistent differences in the incidence of starvation between fish taken from areas of high larval density and those taken from areas of low larval density (Fig. 15). Therefore, to estimate mortality due to starvation, I combined all samples collected in the offshore area. To estimate mortality rates on a daily basis, the observed number of fish belong-

TABLE 4.—Histological condition of jack mackerel collected 350 km off the coast of California.

	Dying	Starving	Recovering	Healthy	Total	Daily percent Starving[1]	Daily percent Dying[2]
Yolk sac	—	—	—	15	15	0	0
<3.5 mm							
Number	43	74	45	38	200		
Duration (d)	1	3	2	6			
Number/d	43	24.7	22.5	6.3	96.5	70	45
3.5-<4.0 mm							
Number	2	16	38	54	110		
Duration (d)	1	3	2	3.3			
Number/d	2	5.3	19	16.4	42.7	17	5
4.0-<4.5 mm							
Number	0	2	12	45	59		
Duration (d)	—	3	2	3.3			
Number/d	—	0.7	6	13.6	20.3	3	0

[1] $\frac{\text{Number dying/d + starving/d}}{\text{Total}}$

[2] $\frac{\text{Number dying/d}}{\text{Total}}$

ing to each size and health category was divided by the duration—the number of days jack mackerel are expected to remain in each category (Table 4). Durations spanned 1 to 6 d depending on age and condition. For healthy fish, duration is simply the size-class interval divided by the growth rate. Healthy fish belonging to the smallest size group (<3.5 mm) grow at 0.05 mm/d (Theilacker 1978) and begin to eat at 3.2 mm SL. Thus duration for this size interval (0.3 mm) was 6 d. Growth rate for older fish was 0.15 mm/d; the rate was determined for this study by counting daily growth increments in otoliths (Hewitt et al. in press). The duration that a larva remains in one of the starvation states is a function of the persistence of the histological criteria. Young jack mackerel deprived of food in the laboratory show signs of starvation for 3 d before dying, and larvae recovering from a period of starvation show these signs for 2 d (Theilacker 1978, 1981). Older fish may be more resistant to starvation, but as I had no information for older jack mackerel, I used the durations for younger larvae.

For the smallest jack mackerel living 350 km offshore, 45% were dying of starvation per day. Daily mortality dropped rapidly to 5% to zero for older larvae (Table 4). Increasing the durations for the older larvae in the starving and recovering categories (Table 4) decreases this estimate of daily mortality.

Results of the histological examination of jack mackerel collected near islands and banks allow a preliminary assessment of the effects of different habitats on starvation (Table 5; Fig. 16). A large difference existed in the daily larval mortality caused by starvation between the open ocean and island and bank habitats. In areas near the islands, none of the first-feeding larvae were dying of starvation whereas 45% from the open ocean were dying of starvation. In addition, healthy larvae taken near islands were apparently more fit than healthy larvae captured in the open ocean, as the larvae from the island habitats had abundant quantities of glycogen in the liver (Fig. 10), whereas livers of larvae from the open ocean rarely contained glycogen stores (Fig. 9). This indicates that food must have been much more abundant in the island habitat because not only were fewer fish starving but the healthy fish were able to store glycogen. The healthy fish from the open sea may have been just able to meet their daily metabolic requirements.

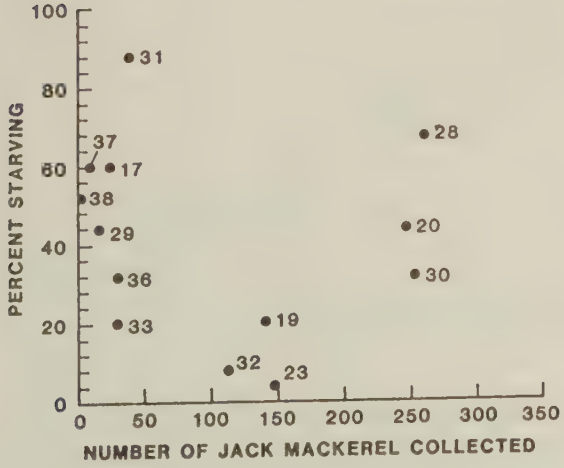

FIGURE 15.—Percentage of starving *Trachurus symmetricus* larvae (number starving/number analyzed) related to the number of larvae collected at each offshore station; station number is indicated.

The morphological data gave essentially the same results as did the histological method. On the basis of morphometric evidence, 70% of the first-feeding jack mackerel (<3.5 mm SL) were starving and the number decreased to zero for older jack mackerel (Table 6). Although the results were similar, the morphological categories used to classify the fish were different from the histological ones. In particular, there was no morphological category for dying fish. For the morphometric SWDA, larvae were grouped by feeding treatment (Table 6), and the histological categories (Table 4) were based on the dominant larval tissue conditions determined to characterize a nutritional state. Thus the morphometric SWDA cannot be used to estimate the number of larvae dying per day due to starvation.

DISCUSSION

Larval Starvation and Recruitment

Both histological and morphological criteria indicate that starvation is probably a major source of larval jack mackerel mortality at the time of first-feeding but that the survivors of this 6-d period are much less vulnerable to starvation. Prey (mainly young stages of copepods) are more abundant at the nearshore islands and banks off the coast of California than offshore (Beers and Stewart 1967, 1970; Arthur 1976, 1977; Devonald 1983), and survival of first-feeding jack mackerel was higher in the nearshore habitats than offshore. Thus selection of spawning sites may have a great effect on survival. Eggs and larvae of jack mackerel are very widely distributed; they occur from Baja California to British Columbia and up to 400 mi off the coast of

TABLE 5.—Histological condition of jack mackerel collected near islands and banks off the coast of California.

	Dying	Starving	Recovering	Healthy	Total	Daily percent Starving[1]	Daily percent Dying[2]
Yolk sac	—	—	—	—	0		
<3.5 mm							
Number	0	2	6	12	20		
Duration (d)	1	3	2	6			
Number/d	—	0.7	3	2	5.7	12	0
3.5-<4.0 mm							
Number	0	1	1	12	14		
Duration (d)	1	3	2	3.3			
Number/d	—	0.3	0.5	3.6	4.4	7	0
4.0-<4.5 mm							
Number	0	0	0	7	7		
Duration (d)	1	3	2	3.3			
Number/d	—	—	—	2	2	0	0

[1] $\frac{\text{Number dying/d + starving/d}}{\text{Total}}$

[2] $\frac{\text{Number dying/d}}{\text{Total}}$

TABLE 6.—Predicted condition of field-collected jack mackerel larvae determined with the morphometric technique.

	Starved 3 days	Starved 1 & 2 days	Fed	Total	Daily percent Starving[1]
<3.5 mm					
Number	48	66	150	264	
Duration (d)	[2]2	2	6		
Number/d	24	33	25	82	70
3.5-<4.0 mm					
Number	0	1	121	122	
Duration (d)	2	2	3.3		
Number/d	—	0.5	36.7	37.2	1.3
4.0-<4.5 mm					
Number	0	0	59	59	
Duration (d)	2	2	3.3		
Number/d	—	—	17.9	17.9	0

[2] $\frac{\text{Number starved/d}}{\text{Total}}$

[2] Unfed jack mackerel larvae die in 4 d.

California and up to 1,000 mi off Oregon and Washington (reviewed by MacCall and Stauffer 1983). In addition, jack mackerel have a protracted spawning season which extends from March through September. The bank and island habitat must be a very small fraction of the total spawning habitat; thus despite the higher survival in inshore areas, the offshore zone may be the most important. In addition, better feeding conditions around islands may be offset by a greater abundance of predators. Whether the large concentration of starving larval jack mackerel found offshore was an isolated case or a general condition in offshore areas is unknown. Given that relative recruitment strength of jack mackerel year classes varies greatly and is rarely "average" (Fig. 17; MacCall and Stauffer 1983), the daily mortality rate of about 45% found in this study is not unrealistic. Considering the relatively long lifetime (i.e., 30+ yr) and high fecundity of jack mackerel, one can deduce that the overall mortality may be very high. This study certainly indicates that starvation at the onset of feeding may be an important factor influencing recruitment variation in jack mackerel.

O'Connell's (1980) study of northern anchovy is the only other study in which starvation in the sea has

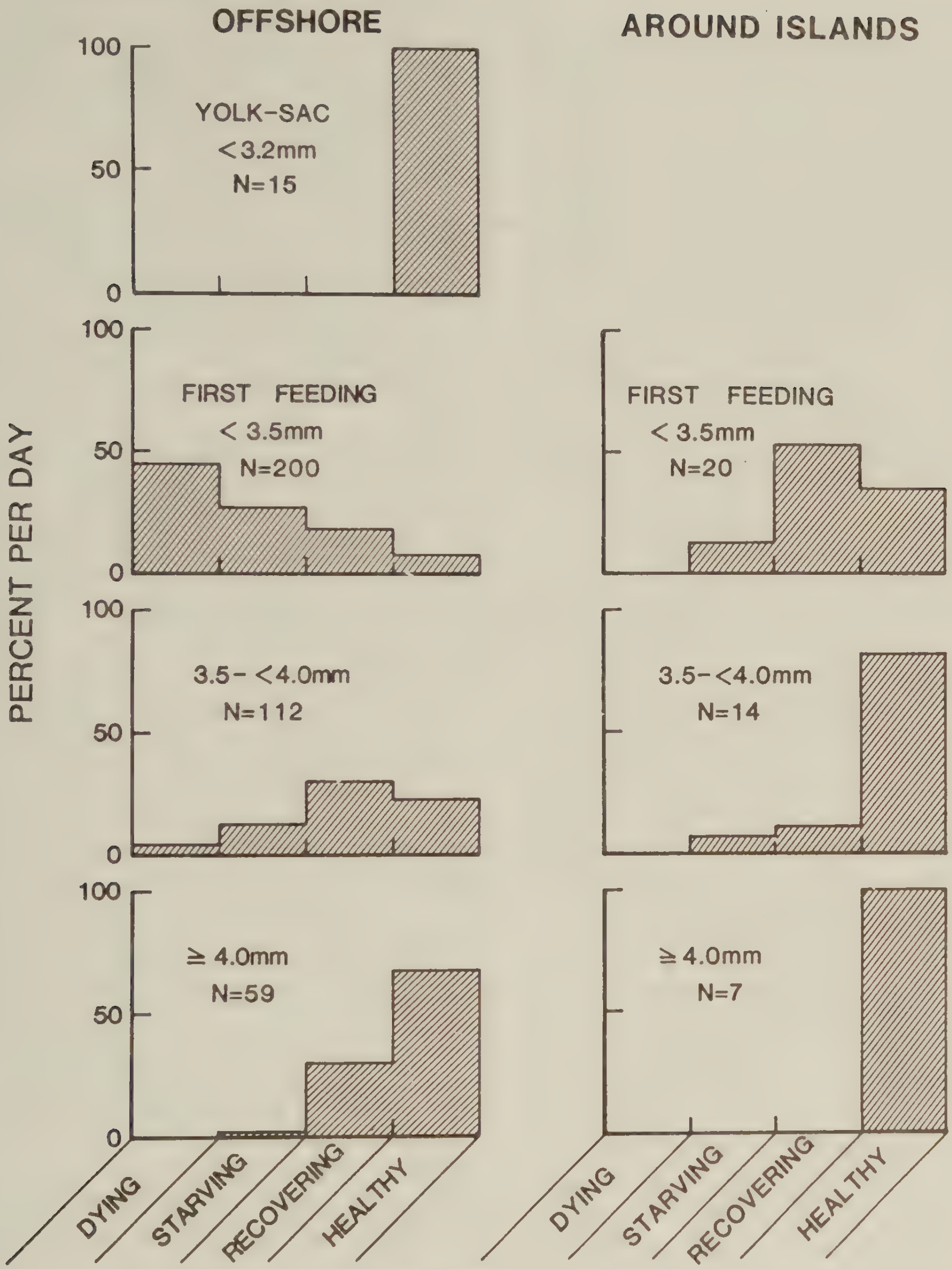

FIGURE 16.—Comparison of the nutritional condition of young *Trachurus symmetricus* collected from offshore and nearshore habitats. Daily percents taken from Tables 2 and 3.

been assessed using histological criteria. O'Connell examined 318 northern anchovy larvae from 64 stations that extended over a large area, 20-350 km off the coast of California. To compare the mortality of northern anchovy with the daily rates I found for jack mackerel, I calculated size-specific daily mortality of northern anchovy by using 1) O'Connell's (1980) histological evaluation, 2) information on time to irreversible starvation to determine durations (Lasker et al. 1970; Hunter 1981; Theilacker and Dorsey 1981), 3) information on shrinkage of ocean-caught northern anchovy to determine size at first

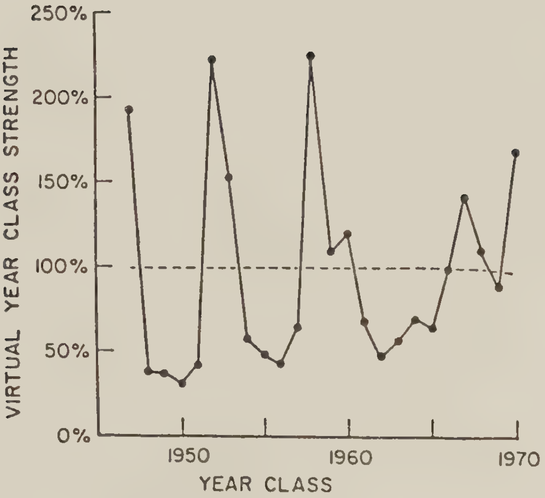

FIGURE 17.—Relative recruitment strengths of jack mackerel year classes in southern California. Virtual year-class strength is measured by the sum of percentage contributions to seasonal landings over the lifetime of the year class. The dashed line indicates average strength (from MacCall and Stauffer 1983; Fig. 4).

feeding (Theilacker 1980a), and 4) a growth rate of 0.37 mm/d for healthy sea-caught northern anchovy (Methot and Kramer 1979). Although the number of first-feeding larvae was low in O'Connell's data ($n = 23$), I calculated a starvation-induced mortality rate of between 35 and 46%/d. Thus my calculations indicate that substantial numbers of northern anchovy larvae as well as jack mackerel larvae are dying at the time of first feeding. This loss rate for northern anchovy is similar to estimated total mortality rate at this stage, 39%/d (Lo in press; 1978 data), which suggests that starvation is the major source of mortality at first feeding. This conclusion for northern anchovy could not be drawn at the time that O'Connell did his work because the data on net shrinkage were not known. The average rates estimated by O'Connell were much lower because he combined larval size classes.

Attempts to assess larval starvation in the sea using morphological criteria are more common (Shelbourne 1957; Honjo et al. 1959; Nakai et al. 1969; reviewed by May 1974; Ehrlich et al. 1976), but they have seldom been successful, probably because of the biases introduced by failure to correct adequately for shrinkage (see next section). Recently Devonald (1983) used a morphometric index with shrinkage adjustments to assess jack mackerel feeding regimes off California. She found good correspondence between jack mackerel condition and prey availability and concluded that feeding conditions were better near islands than in the area between islands. Several of her samples and my samples were taken concurrently (San Clemente and Tanner Bank; Table 1), and I found that 92% of the jack mackerel from the island habitat were healthy. Thus, my results obtained using histological criteria confirm Devonald's conclusion.

Other techniques used in the past to assess food availability include RNA/DNA (Buckley 1980), food in gut (Rojas de Mendiola 1974; Ciechomski and Weiss 1974; Arthur 1976; Ellertsen et al. 1981), and otoliths. Of course otolith work is critical because estimates of growth rates are essential for assessment of mortality, but it is of no value for assessing growth at the onset of feeding (Methot 1981).

Arthur (1976) conducted the only other study on the feeding of jack mackerel off the coast of California. He found, after examining the stomach contents of 750 specimens from 65 offshore samples, that 60% of the first-feeding jack mackerel and 10% of the older larvae (7 mm) had empty stomachs. This observation lends additional credence to my histological evaluation of jack mackerel collected offshore that shows 59% of the first-feeding fish and 3% of the older fish (>4 mm) were starving.

I believe my estimates of jack mackerel mortality due to starvation are conservative. The assumptions I made about the persistence of starvation and the duration of growth were based on extensive laboratory studies (Theilacker 1978, 1981). Because the majority of jack mackerel were collected at sites warmer (16.1°-16.6°C) than the culture temperature (15°-15.5°C), the durations for growth and starvation may be altered, but the final estimate of mortality due to starvation is higher after the appropriate changes to the durations are made. Furthermore, if net retention of robust fish is greater than retention of thin fish of the same length, starvation may be underestimated. In addition, the selection of unhealthy larvae by predators would also increase the starvation estimate.

Previous evidence supporting the occurrence of starving fish larvae in the ocean has been mainly circumstantial (reviewed by May 1974; Jones and Hall 1974; Lasker 1975). Evidence from this study and O'Connell's (1980) study shows that starvation does occur and that the young stages of jack mackerel and northern anchovy are highly vulnerable.

Comparison of Morphological and Histological Criteria for Starvation Diagnosis

The incidence of starvation based on morphological criteria was essentially the same as that based on histological criteria. Owing to the relative ease, and low cost of measuring fish compared with a histological examination, the morphological analysis is an attractive approach. On the other hand, histological analysis defines a cause and effect relation between structure and starvation whereas gross morphological measurements provide an index of starvation which is highly vulnerable to errors and biases in calibration and interpretations. Because of the importance of these measurements in recruitment studies, it is appropriate to consider the merits of and potential errors in these techniques in some detail.

The morphometric approach relies on measurements of fish to compare reared and wild animals at the same developmental stage. Thus shrinkage adjustments are needed to intercalibrate laboratory measurements and field measurements. Fish shrink when collected in a net and preserved, and shrinkage of the size of all body parts is dependent on the time in the net, size of fish, and type of preservative used (Blaxter 1971; Theilacker 1980a; Hay 1981). In this study, tow time was controlled at 5 min and samples were preserved within 8 min. Thus damage to the fish and shrinkage were minimal, but the samples were not quantitative. It is doubtful that the morphometric technique will work with jack mackerel taken in standard, quantitative collections. Quantitative net tows are 20 min, and they include an additional hosing down of the nets before sample preservation (Smith and Richardson 1977). The procedure damages the larvae, causing extensive shrinkage which makes accurate measuring difficult. Further, a long tow time decreases confidence in time-specific shrinkage estimates because fish can be collected at any time during the towing period. Increasing the tow time also causes both the magnitude of the shrinkage correction factor and the standard error of its estimate to increase. For example, in this study, standard length of jack mackerel shrank by an average of 6.0 ± 0.6% in 8 min and 19.0 ± 1.0% in 20 min.

While laboratory calibration is absolutely essential for the morphometric analysis, no shrinkage calibration is needed for the histological analysis, and it might be possible to use the histological observations on other fishes. Diagnostic criteria for the starving condition of jack mackerel (Theilacker 1978), northern anchovy (O'Connell 1976), and yellowtail, *Seriola quinqueradiata*, (Umida and Ochiai 1975) were similar. In addition, important biological information is gained while using the histological approach whereas gross morphological indices provide no such information. For example, histological analysis of jack mackerel has revealed a pattern of diel swim bladder inflation and a disruption of this rhythm, accumulation of glycogen reserves, and brain lesions presumably produced by UV radiation (Hunter et al. 1979). There is just no substitute for this extensive biological information. On the other hand, population work requires large samples, and morphological indices are probably the only practical means for working with very large samples. Thus, the optimal experimental design for population work on starvation is probably the use of morphological criteria (calibrated for shrinkage) combined with a smaller subsample of fish which are graded histologically. All work requires special net tows, preservation, procedures, and laboratory calibration.

Caution needs to be exercised when transferring information obtained in the laboratory to the field. Raising larval jack mackerel in small containers is known to affect growth, nutritive condition, and possibly activity (Theilacker 1980b). Additionally, there is evidence that wild fish tend to be thinner than their laboratory counterparts (larval herring, Blaxter 1971; juvenile herring, Balbontin et al. 1973; larval northern anchovy, Arthur 1976). My use of the morphometric SWDA assumes that the morphometric criteria I developed in the laboratory for larval jack mackerel raised in large tanks are applicable to ocean-caught jack mackerel.

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Use of an ELISPOT immunoassay to detect euphausiid predation on larval anchovy

Gail H. Theilacker[1], Amy S. Kimball[1] & James S. Trimmer[2]

[1] National Marine Fisheries Service, Southwest Fisheries Center, 8604 La Jolla Shores Drive, La Jolla, California 92038, USA
[2] Scripps Institution of Oceanography, University of California San Diego, La Jolla, California 92093, USA

ABSTRACT: The ELISPOT immunoassay, where samples are spotted onto 0.45 µm pore-size nitrocellulose and incubations are based on a BLOTTO/Tween system, proved satisfactory for detecting northern anchovy *Engraulis mordax* yolk in euphausiid *Euphausia pacifica* guts. Polyclonal antiserum to anchovy yolk was developed in male New Zealand rabbits. The system detected 30 nannograms purified yolk protein with 1:5000 diluted antiserum and positively identified 75 % of experimentally-fed and frozen euphausiids.

INTRODUCTION

Euphausiids, copepods, amphipods, and other small Crustacea potentially prey on the earliest stages of marine fish larvae (reviewed by Hunter 1981, 1984, Brewer et al. 1984). Euphausiids, for example, co-occur in the sea with northern anchovy larvae, and in the laboratory individual euphausiids consume up to 25 larvae d^{-1} (Theilacker & Lasker 1974). Thus if this predation rate occurs in the sea, euphausiids could be responsible for an important portion of the mortality of yolk-sac anchovy larvae as well as other fish larvae. Because Crustacea macerate their prey, it is impossible to visually identify larval remains in the stomachs of wild Crustacea. Two possible solutions to this problem are to use larval eye lenses to identify the larval remains (Purcell 1984) or to use immunoassays designed to detect species-specific proteins (Boreham & Ohiagu 1978, Calver 1984). Here we evaluate the use of an immunoassay to detect larval northern anchovy *Engraulis mordax* remains in euphausiid *Euphausia pacifica* stomachs.

Serological precipitation and agglutination reactions have been used in other predator-prey studies. Boreham & Ohiagu (1978) reviewed and evaluated studies that used serological techniques to describe invertebrate (mainly economically important insects) predator-prey relations and predation rates. Feller et al. (1979) applied serological techniques to describe food web relations in a benthic community. These tests required large quantities of the unknown stomach samples and serum. More recently developed radioimmunoassays (RIA) (Heusser et al. 1981) and enzyme-linked immunosorbent assays (ELISA) (Engvall & Perlmann 1972) require small samples, are extremely sensitive and are quantitative. Crook & Sunderland (1984) used ELISA to detect the ingestion of aphids by predatory spiders. We selected the solid-phase enzyme-linked immunospot (ELISPOT) (Monroe 1985) because, in addition to being an ultrasensitive technique, it was the most effective procedure for assaying many small samples. We prepared a polyclonal antiserum to anchovy egg yolk proteins because previous laboratory work indicated that only yolk-sac stage larvae were vulnerable to euphausiids (Theilacker & Lasker 1974). The sensitivity of the ELISPOT and antiserum was tested by assaying euphausiids fed yolk-sac anchovy larvae in the laboratory.

METHODS

Feeding. Euphausiids collected off the coast of California from the NOAA Ship *David Starr Jordan* were maintained in the laboratory at 15.5 to 16.0 °C (Lasker & Theilacker 1965) and fed the alga *Dunaliella tertiolecta* to clear their guts 24 or more h before a feeding test. For feeding tests, single euphausiids were placed into 250 to 750 ml sea water containing 25 to 50 yolk-sac larvae. After euphausiids fed for 2 to 3 h, they were frozen individually in liquid nitrogen, and larval anchovy prey remaining in the containers were counted to determine the number eaten.

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Preparation of antigen. To obtain anchovy yolk proteins for the antigen, we separated the yolk from egg membranes and vacuoles by washing freshly spawned anchovy eggs in 0.45 µm filtered sea water and hand homogenizing them in 10 mM phosphate buffer pH 7.4 with 3 to 4 strokes in a glass tissue homogenizer on ice (R. A. Wallace pers. comm.). The solution was spun for 5 min in an Eppendorf microfuge (15600 × g). The supernatant, containing 18 mg ml^{-1} protein (method by Lowry et al. 1951), was frozen at −80 °C in 500 µl aliquots for use in rabbit injection (see 'Preparation of antisera'), titre tests, and as internal standards.

Preparation of antisera. Two male New Zealand White rabbits were bled twice before immunization. The bleeds were from the central ear artery and were 7 d apart; each rabbit gave a total of 70 ml blood. For these bleeds and all subsequent bleeds, we allowed blood to clot for 35 min in a centrifuge tube at room temperature, rung once with a glass stirring rod (Hurn & Chantler 1980) and centrifuged at 2000 × g for 10 min. We removed the serum fraction and froze it at −80 °C in 500 µl aliquots.

The schedule for injecting the rabbits was based on Vaitukaitus (1981) in which microgram amounts of antigen were used to produce antisera with high titre. The first injection was given 12 d after the second pre-immune bleed. We diluted yolk preparation in 10 mM phosphate buffer pH 7.4 and emulsified in 3 volumes Freund's complete adjuvant on ice using a Brinkmann Polytron homogenizer on low to medium speed for 15 s. An emulsification containing 180 µg yolk in 1 ml was injected into 8 intradermal sites (0.125 ml $site^{-1}$) on a shaved region of each rabbit's back adjacent to the spine. The first antiserum was collected on Day 24. Rabbits were 'boosted' with 0.5 ml emulsification containing 45 µg yolk in Freund's incomplete adjuvant on Day 44 and again 6 mo later. The final bleed was taken 10 mo after the first injection.

ELISPOT. We placed individual euphausiids stored at −80 °C in 15 µl extraction buffer (10 mM Tris hydroxymethyl aminomethane hydrochloride [Tris-HCl] pH 7.4, 1 mM ethylenediaminetetraacetic acid [EDTA]) on a clean microscope slide and, using a dissecting microscope at 6× to 25×, dissected the euphausiid stomach, hindgut, hepatopancreas and mouthparts. These tissues were teased apart and extracted in the buffer prior to dotting 10 µl of this protein extract onto nitrocellulose paper (0.45 µm pore size). We have stored these protein extracts on the nitrocellulose for up to 4 d at 3 °C with no loss in activity. Dotted nitrocellulose was blocked by incubating 1 h in 25 ml BLOTTO/Tween (5 % dry nonfat milk in 0.45 µm filtered sea water; 0.01 % Antifoam A; 0.0001 % merthiolate; 0.05 % polyoxyethylene [20] sorbitan monolaurate [Tween 20]; Johnson et al. 1984). This was followed by 1 h incubation in the primary antibody, 1:5000 rabbit serum (pre-immune or immune) diluted in 5 ml BLOTTO/Tween. A series of 3 detergent washes followed the primary antibody incubation (first wash [3 × 10 min], 0.5 M NaCl; 10 mM Tris-HCl, pH 8.2; 0.5 % Nonidet P-40; 1 mM EDTA; 1 mg ml^{-1} nonfat milk; 0.1 % Lauryl sulfate [SDS]; second wash [3 × 10 min], substitute 0.15M NaCl for 0.5 M in first wash and eliminate milk; third wash [3 × 10 min], equivalent to second wash without SDS; Trimmer et al. 1985). After the washes the samples were blocked in 3 % normal goat serum in 5 ml BLOTTO/Tween for 20 min and then incubated for 1 h with 3 % normal goat serum and the secondary antibody, 1:1000 Goat Anti-rabbit conjugated alkaline phosphatase (Blake et al. 1984), in 5 ml BLOTTO/Tween. After incubation with the secondary antibody, the samples were washed 4 × 10 min in BLOTTO/Tween followed by a 10 min wash in 0.15 M Tris-Base pH 9.6. Reactions were done using 47 mm diameter nitrocellulose filters in beakers on a shaker. Each assay was run using at least one 5 µl spot of anchovy yolk protein (0.03 µg to 1 µg per 5 µl spot) and the extract of one starved euphausiid control dotted on the nitrocellulose as internal standards for the pre-immune and immune sera.

The alkaline phosphatase activity was visualized on the nitrocellulose with a histochemical phosphatase stain (1 mg 5-bromo-4-chloro-3-indolyl phosphate dissolved in dimethyl formamide; 2 mg nitro blue tetrazolium dissolved in 0.15 M Tris-Base pH 9.6; 4 mM $MgCl_2$; brought to 20 ml with 0.15 M Tris-Base pH 9.6; Blake et al. 1984, Knecht & Dimond 1984). A positive reaction was a blue/black color and the color intensity corresponded to the amount of yolk protein present. All chemicals used were of highest quality.

RESULTS AND DISCUSSION

Titre of the antiserum increased 12 times after the second injection and an additional 3 times after the third injection. The final antiserum diluted 1:20000 detected 0.1 µg yolk protein. We routinely used a 1:5000 dilution which detected 0.03 µg yolk protein. Undiluted sera were stable at 3 °C for at least 1 mo (no azide or merthiolate present).

Antisera harvested early in the experiment are believed to be more specific (yielding fewer cross-reacting antibodies) than antisera harvested later in the experiment (Vaitukaitus 1981); we found no difference in nonspecific binding to euphausiid muscle between antisera collected over 10 mo. To determine the specificity of the antisera to anchovy yolk proteins, we tested various potential euphausiid foods for cross-reactions. The final antisera did not react with the algae *Gymnodinium splendens, Dunaliella* sp., *Monochrusis* sp., the copepod *Tigriopus californicus*, eggs of the red crab, *Pleuroncodes*, and eggs of the sea urchin, *Strongylocentrotus purpuratus*. The serum also did not cross-react with white sea bass *Atactoscion nobilis* yolk protein but did cross-react with egg yolk from the sardine *Sardinops sagax*, indicating that the serum may not discriminate between clupeoid yolk proteins in general. This cross-reaction could perhaps be removed by absorption (Boreham & Ohiagu 1978). As live fish eggs become available, we will determine the ability of the antibody to discriminate between teleosts. In all tests the pre-immune controls were nonreactive.

Proteins from the yolk preparation and similar preparations of developing anchovy eggs and larvae, Days 2 to 6, were analysed by SDS-polyacrylamide gel electrophoresis (SDS-PAGE, 10 %; Maizel 1971). Seven Coomassie staining bands of Mr = 16700, 18200, 28200, 30300, 72900, 80700 and 91200 were present in the yolk preparation but not in post yolk-sac larvae. Proteins from the yolk-sac preparation and the post yolk-sac larvae, separated on 10 % SDS-PAGE, were transferred to nitrocellulose paper (Towbin et al. 1979) and reacted with immune and pre-immune serum using the incubations and washes of the ELISPOT procedure. Three yolk bands (Mr = 72900, 80700 and 91200) reacted with the first antisera; the antisera did not react with the non-yolk anchovy proteins. The ELISPOT revealed that the reactivity of the yolk proteins with the antisera was maintained during egg and larval development.

Yolk preparations were stable, maintaining their reactivity for at least 1 mo at 3 °C when stored in concentrated forms. Ability of buffer systems to maintain ingested yolk protein stability was determined by incubating 10 µg of yolk protein with buffer homogenates of the euphausiid stomach and hepatopancreas for 15 and 60 min at 12 °C. These tests revealed that the Tris/EDTA extraction buffer maintained yolk protein stability better than millipore filtered sea water or phosphate-buffered saline (0.01 M $NaH_2PO_4 \cdot H_2O$, 0.15 M NaCl, pH 7.2) and that protease inhibitors (phenyl methyl sulfonyl fluoride, soybean trypsin inhibitor) and competitors (benzamidine, bovine serum albumin; BSA) did not increase stability.

When testing RIA and ELISA, we found that we were losing samples from the plastic wells during the washes. This did not appear to be a problem in the case of nitrocellulose paper.

To eliminate nonspecific binding of the antiserum to the muscle protein of starved euphausiids in the ELISPOT assays we tried dissecting the digestive tissues from the animal. Dissecting decreased the cross-reaction obtained by testing whole animal extracts. We also reduced this unwanted reaction to a negligible level by using the BLOTTO technique of Johnson et al. (1984) to block nonspecific protein binding sites on the nitrocellulose, to carry the antibodies, and as the washing solution instead of using BSA or gelatin. The addition of the detergent Tween-20 to the BLOTTO buffer, a series of rigorous washes (high-salt, low-salt detergent washes) and an incubation in 3 % NGS (see ELISPOT) also significantly reduced the background. Dialyzing the antisera in sea water did not improve the assay.

Initially we used horseradish peroxidase as the conjugate (GAR/HRP; goat antirabbit horseradish peroxidase) for the secondary antibody with Aminoethyl-carbazole as the substrate (Podell & Vaquier 1984). We found that extracts from euphausiid preparations gave the same pink/brown color (astaxanthin pigment; Mauchline & Fisher 1969) when dotted onto the nitrocellulose as the final visualization of the GAR/HRP reaction. Solvent extractions of the pigment prior to ELISPOT were unsatisfactory because the lipophilic yolk proteins were also extracted. Visualization of an alkaline phosphatase (GAR/AP) conjugate of the secondary antibody produced a blue/black color that is easily differentiated from the pigment spot.

Using ELISPOT we tested 56 laboratory-fed euphausiids for the presence of anchovy yolk and of these 42 animals were positive. No response may be due in part to loss of yolk protein from the yolk sac when the euphausiid grasps and macerates the larva. On the other hand, gastric evacuation rates of larvae in euphausiid stomachs may be very high, with complete evacuation occurring within the experimental feeding period. Preliminary experiments show that yolk protein is digested in less than 4 h. We calculated that the stomach of a 20 mm euphausiid which consumed one yolk-sac anchovy could contain as much as 1.8 µg anchovy yolk protein (volume of a euphausiid stomach is about 0.06 mm^3; a full stomach holds 60 µg wet weight or about 6 µg dry weight for prey containing 90 % water; the dry weight of a Day 2 yolk-sac anchovy is 21 µg and 30 % of the dry weight is yolk protein; 30 % of the maximum euphausiid stomach contents [6 µg] is 1.8 µg) but the ELISPOT assay rarely detected more than 0.3 µg in stomachs of the euphausiids fed in the laboratory. Thus it appears the reactivity of the antisera to anchovy yolk proteins may be reduced *in vivo*.

The ELISPOT assay is a quantitative technique, although application of the assay in the field cannot be quantified here because the absolute amount of yolk in an individual anchovy decreases with age and because the reactivity of the yolk protein to the antisera apparently decreases *in vivo*. However, we can estimate the impact of euphausiid predation on larval anchovy by determining the positive euphausiid antigen-antibody reactions and adjusting for their size-specific feeding rates, their temperature-specific digestion time, their size-specific abundance, and relating the estimated extent of predation to the abundance of larval anchovy.

A proposed predation study, part of an integrated study of the northern anchovy habitat off southern California, will yield quantitative information on the total number of larval fish taken, the proportion of anchovy larvae, and the size-specific abundance of *Euphausia pacifica*. Much additional information has been published by Brinton (1962, 1967, 1976, Brinton & Wyllie 1976) on the seasonal abundance and vertical distribution of all *E. pacifica* growth stages in the California Current. Theilacker & Lasker (1974) reported on laboratory studies of size-specific feeding rates of *E. pacifica* on larval anchovy, and the immunoassay will yield information on the presence of anchovy yolk protein in *E. pacifica* guts that can be related to their size. Preliminary experiments show that the yolk protein is labile; activity cannot be detected in euphausiid guts after a digestion time of 4 h. The 2.5 mm mesh net used to collect the euphausiids does not catch potential euphausiid prey, thus avoiding the possibility of euphausiids feeding while in the net. Nicol (1984) showed that feeding in the net by the euphausiid *Meganyctiphanes norvegica* caused significant error. Unfortunately, we have the problem of unknown cross-reactions with yolk from other larval fish. However, in the area that we intend to study off the coast of California, northern anchovy larvae are the most abundant larval fish, comprising about 80 % of the total larval fish taken in recent annual surveys (Loeb et al. 1983, H. G. Moser pers. comm.).

Application of an immunoassay in the field to assay the gut contents of small, predatory Crustacea requires an extremely sensitive technique because of the small sample size and the probability of reduced antisera reactivity with digested yolk protein. The highly sensitive ELISPOT assay measured nannogram quantities of anchovy yolk protein in euphausiid guts. In addition, ELISPOT is easy to perform, taking about 6 h to complete. The number of predators that can be tested in a day is limited by the number of animal dissections that can be performed in a day. A stomach dissection takes about 6 min, and stomach contents spotted on nitrocellulose can be stored in the refrigerator up to 4 d, possibly longer, with no loss in activity. Thus the ELISPOT assay could be applied to large-scale field studies to provide information on predation mortality of larval fishes that is needed to refine recruitment estimates.

For interested persons, antibody is available from the senior author.

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86109

BERYCIDAE — Alfonsin

by Richard N. Uchida

Valid name	*Beryx splendens* Lowe 1833 (Fig. 47)
Synonymy	None
Common names	Alfonsines; alfonsin; alfonsino

Distribution

Caught only at Hancock Seamounts and Banks 10 and 11 in the NWHI between depths of 258 and 302 m.[7]

Distinguishing characteristics

D. IV, 13-15, A. IV, 26-29; P1. 17-18. Body elongate, compressed, bright red, and covered with moderate-sized ctenoid scales which are rather stiff and prickly giving the body a rough texture. Head large, compressed, eyes large. Snout blunt, mouth sharply oblique, and the lower jaw protruding beyond the snout. Small teeth in bands on jaw. Inside of mouth scarlet. A small spine anterior to the orbit projecting posteriorly.

A congener, *B. decadactylus* Cuvier and Valenciennes 1829, also occurs in Hawaiian waters from Hancock Seamounts to the major islands in the southeast end of the chain. Meristic counts are: D. IV, 16-20, A. III-IV, 27-30; P1. 16-18; P2. I, 9-10. *Beryx decadactylus* differs morphologically from *B. splendens* by having much larger and rougher scales, stronger more prominent preorbital spine, and deeper body. Body color of *B. decadactylus* is brighter than that of *B. splendens*.

Life history

Alfonsin spawn in August-October and the free floating eggs hatch in about 1 day. Newly hatched larvae are planktonic and float for about 2-3 days before they begin to swim on the fourth day (Onishi 1967; Chikuni 1971). In the western Pacific, the distribution of this species is highly dependent on the Kuroshio and its fractional systems.

Berycoid fishes assume a demersal existence at age 1 year or younger. Japanese studies indicate that they migrate from coastal waters to offshore grounds and that fish size increases with depth and decreases with increasing latitude (Kanagawa Prefectural Fisheries Experimental Station 1971). Alfonsin migrate vertically in the evening (Masuda et al. 1975) presumably to feed on surface dwelling organisms. Stomach analysis of fish taken over the Emperor Seamounts disclosed that small fish predominated in the diet; crustaceans including decapods, mysids, and euphausiids constituted almost all the remainder (Aomori Prefectural Fisheries Experimental Station 1976).

Alfonsin captured by NMFS at Hancock Seamounts ranged from 15.3 to 35.3 cm fork length (FL), whereas over all the central North Pacific seamounts, the size range was 13.0 to 46.0 cm FL (Takahashi and Sasaki 1977). Apparently, the number of age groups in the catch varies from year to year and among seamounts. In 1972, for example, fish captured at the Milwaukee Seamount group had modes at 21.0 and 38.0 cm; whereas fish taken at Colahan Seamount had one mode at 19.0 cm. The age-length relationship for alfonsin is as follows: age 1 = 8.8 cm; age 2 = 19.1 cm; age 3 = 25.8 cm; age 4 = 30.8 cm; and age 5 = 32.8 cm (Ikenouye 1969).

Gear and catch

In addition to bottom trawls, in which it is mostly a by-catch of fishing for pelagic armorhead, alfonsin is also taken by bottom longline and handline. The species rarely enters baited traps.

Annual catches of alfonsin in the Japanese trawl fishery at Hancock Seamounts in 1969-81 varied from 0 to 54 MT and averaged 8 MT. On seamounts located outside the Hawaiian Archipelago, the annual catches of alfonsin varied from 0 to as much as 8,628 MT, averaging about 2,151 MT.

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[7] *Townsend Cromwell* cruise report TC-83-02. *Beryx splendens* were taken at Banks 10 and 11 in depths ranging from 274 to 549 m.

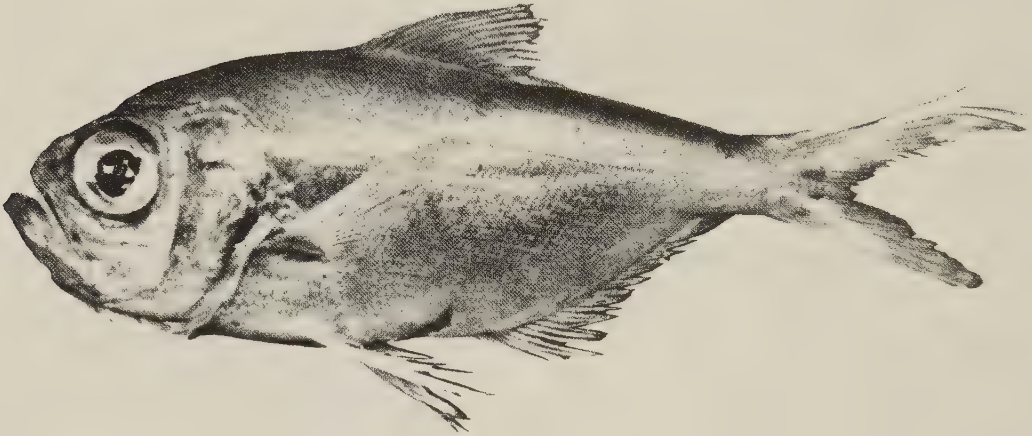

Figure 47.—*Beryx splendens*.

86110

HOLOCENTRIDAE — Uu

by Richard N. Uchida

Valid name	*Myripristis berndti* Jordan and Evermann 1905 (Fig. 48)
Synonymy	*Myripristis murdjan* Randall 1973 *Myripristis amaenus* Fournanoir and Laboute 1976 (from Randall and Guézé 1981)
Common and vernacular names	Red squirrelfish; mempachi; uu

Distribution

Common in the main islands; captured from Nihoa to Kure Atoll in the NWHI.

Distinguishing characteristics

D. X-I, 14; IV, 12; P1. II, 15; P2. I, 7; LLs. 28-31; Gr. 11-14 + 23-28 (Randall and Guézé 1981). Body elongate, rather deep, compressed; head large; snout blunt, convex, its width about twice its length; eyes large, high, upper rims hardly impinging on upper profile of head; eye diameter slightly less than posterior part of head; mouth large, oblique; mandible of adult slightly projecting when closed; maxillary not reaching posteriorly to below posterior margin of eye; several enlarged and blunt teeth on outer front edge of jaws; teeth fine, in broad bands on jaws, vomer, and palatines. Tongue thick, pointed, and in front (Jordan and Evermann 1905).

Lips thick, fleshy; nostrils close together, bones on head finely serrated; opercle with well-developed spine; gill opening large; gill rakers long, fine; caudal forked, pectorals small; scales large, ctenoid, deep on middle of side; lateral line obliquely curved at first, then running obliquely down to base of caudal (Jordan and Evermann 1905).

Color in life red, center of each scale pale, a black bar across opercular region down to axil of pectoral; spines in first dorsal pink and membranes of basal half translucent, upper half orange-yellow; soft dorsal, anal, and caudal crimson but first rays white in each; pectoral red (Jordan and Evermann 1905).

Life history

Hiding in holes and cracks in reefs primarily in the subsurge zone, uu are a nocturnal planktivores feeding mainly on crab megalops and other crustaceans (Gosline 1965; Hobson 1972, 1974). Apparently fishes form an insignificant part of the diet for members of the squirrelfish family (Randall 1967). They emerge from their daytime reef shelter about 30 min after sunset and aggregate in the water column above the reef (Hobson 1972, 1974). Almost immediately after aggregating, they migrate offshore, possibly to the drop-off zone into deep water, which is a major feeding ground for diurnal planktivores (Hobson 1972). The offshore movement may be obscured because many individuals remain over the inshore reef. However, since there are consistently fewer uu over the reefs when there is no moon than on moonlit nights many may be moving offshore, especially on dark nights. About 40 min before sunrise, uu begin to reassemble over the reef and all the individuals take cover within 10 min (Hobson 1974).

Myripristis spp. hunt prey in the water column. This feeding habit is reflected by the sharply upturned mouth, a feature which is highly adapted for feeding on plankton (Hobson 1974). Studies on *M. leiognathus* (Hobson 1965, 1968) and *M. jacobus* (Randall 1980) indicate similar forage patterns.

Gear and catch

Uu are caught mainly by handline; smaller quantities are landed by net and spear fishermen. The species is also taken by trolling at night in relatively shallow water.

Highly prized as a food fish, *Myripristis* spp. (all species) are target species of not only commercial but also recreational fishermen. The State landings of *Myripristis* spp. in 1961-69 fluctuated over a relatively narrow range from 4,330 to 7,449 kg and averaged 5,830 kg. From 1970 through 1976, the catches rose slightly varying between 7,433 and 11,090 kg averaging 9,140 kg. In 1977-79, however, catches rose substantially and landings reached 21,003 kg in 1977, 23,546 kg in 1978, and 20,469 kg in 1979, averaging 21,673 kg. Landings increased in 1977 when speared fish were allowed to be sold.

There is no fishery for uu in the NWHI.

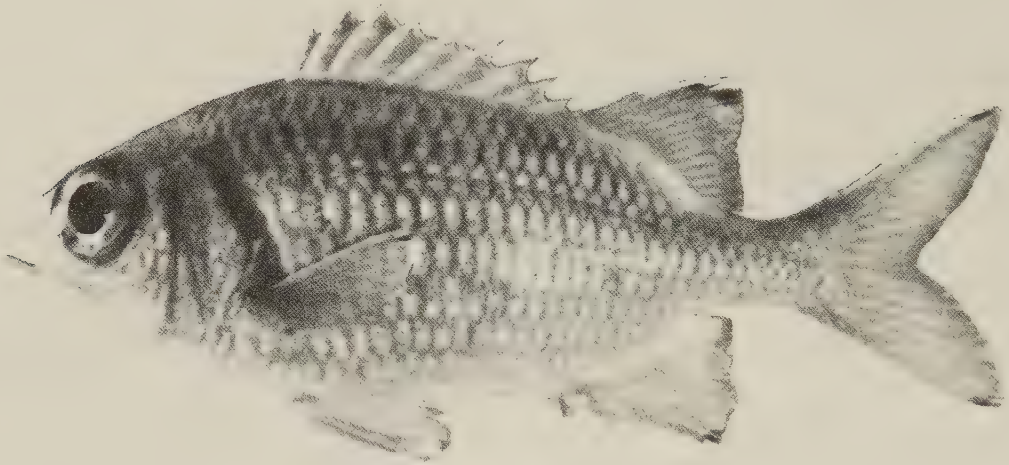

Figure 48.—*Myripristis berndti*.

86111

LUTJANIDAE — Taape

by Richard N. Uchida

Valid name	*Lutjanus kasmira* (Forsskål 1775) (Fig. 63)
Synonymy	*Sciaena kasmira* Forsskåal 1775 *Honocentrus quinquelinearis* Bloch 1790 *Holocentrus quinquelineatus* Bloch 1790 *Holocentrus bengalensis* Bloch 1790 *Diacope octolineata* Cuvier and Valenciennes 1828 *Diacope notata* Cuvier and Valenciennes 1828 *Diacope decemlineata* Cuvier and Valenciennes 1830 *Mesoprion octolineatus* Bleeker 1849 *Mesoprion pomacanthus* Bleeker 1855 *Genyoroge bengalensis* Günther 1859 *Evoplites pomacanthus* Gill 1862 *Mesoprion bengalensis* Kner 1865 *Lutjanus pomacanthus* Bleeker 1868 *Lutjanus bengalensis* Bleeker 1868 *Genyoroge amboinensis* Day 1870 *Diacope Kasmira* Klunzinger 1870 *Lutjanus quinquelineatus* Bleeker 1873 *Lutjanus quinquelinearis* Day 1888 *Mesoprion kasmira* Klunzinger 1884 *Diacope octolineata* Sauvage 1891 *Evoplites kasmira* Jordan and Evermann 1898 *Evoplites decemlineatus* Fowler 1904 *Lutjanus caeruleolineatus* Jordan and Seale 1906 *Lutjanus notatus* McCulloch 1929 *Lutjanus spilurus* Fowler 1931 (from Weber and De Beaufort 1936)
Common and vernacular names	Blue-striped snapper; blue-banded sea perch; blue-line snapper; taape

Distribution

Introduced by the Hawaii DLNR into Hawaiian waters from the Marquesas Islands and Moorea in 1955 and 1961. Opened to public fishing in October 1966 after it became established ([Hawaii] 1967). Now occurs at all major islands and the lower NWHI. The NMFS surveys found taape distributed from Middle Bank to Maro Reef in depths from 24 to 110 m. The range of this species has extended to Laysan (Parrish et al. 1980).

Distinguishing characteristics

D. X-XI, 13-16; A. III, 8; Pl. II, 14-15; LLs. 48-51; Gr. 7+1+14. Body moderately compressed; teeth in jaw in narrow bands, outer series enlarged, anterior ones caninoid; vomer with broad inverted V-shape patch of villiform teeth; knob of interopercle fits into notch on preopercle; scale rows above lateral line running obliquely to base of dorsal fin, those below horizontal; caudal fin emarginate (Schultz et al. 1953; Munro 1967).

Color in life vivid, varying from bright golden to lemon yellow with four blue stripes, edged in deep violet, running lengthwise from head to tail; fins and tail yellowish; blackish blotch sometimes present between front of soft dorsal base and lateral line.

Life history

Not much is known about the reproductive cycle of this species. The rapid spread of taape throughout the main islands and into the NWHI indicates that the eggs and larvae are free floating and are carried by ocean currents between the islands.

The species is an active nocturnal carnivore feeding on or near the bottom. Fish and a few species of adult crustaceans, mainly portunids, constitute the main prey items (Oda and Parrish 1981; Tabata 1981). Despite assertions that taape compete for food with other commercially valuable species such as mempachi, *Myripristis kuntee*, or weke, *Mulloides flavolineatus*, the diets of taape and mempachi caught incidentally with taape did not overlap. Mempachi fed mainly on crab megalops and other planktonic crustaceans.

Taape usually occurs in dense schools as evidenced by our trap catches, which frequently included 100-200 fish per trap in an overnight set. Talbot (1960) reported that off South Africa, females were mature at 125 mm and males with sperm were observed at 155 mm and were ripe at 165 mm.

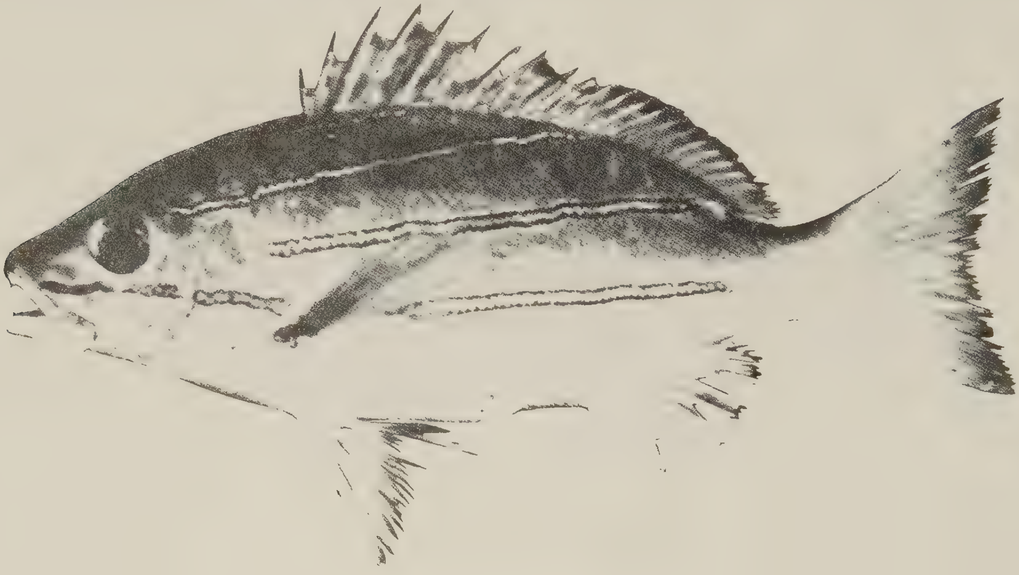

Figure 63.—*Lutjanus kasmira.*

Gear and catch

Usually caught nearshore, the species is harvested by a variety of gear including gill net, handline, rod and reel, purse seine, and traps.

Catches of taape were first reported in 1970 when about 500 kg were landed. By 1977, landings had multiplied nearly 33 times that of 1970, reaching 16,330 kg. The catch continued to increase sharply in 1978, amounting to 26,808 kg, but slowed its increase in 1979 when 27,397 kg were landed.

86112

MULLIDAE — Moano

by Richard N. Uchida

Valid name	*Parupeneus multifasciatus* (Quoy and Gaimard 1824) (Fig. 67)
Synonymy	*Mullus multifasciatus* Quoy and Gaimard 1824 *Pseudupeneus multifasciatus* Jenkins 1902 *Upeneus multifasciatus* Fowler 1922 *Mullus trifasciatus* (not Lacepède) Cuvier 1829 *Upeneus trifasciatus* Lay and Bennett 1839 *Upeneus velifer* Smith and Swain 1882 *Upeneus bifasciatus* (not Lacepède) Sauvage 1891 *Upenoides vittatus* (not Forsskål) Sauvage 1891 *Parupeneus trifasciatus* Steindachner 1901 (from Fowler 1933)
Common and vernacular names	Red and black banded goatfish; moano

Distribution

Occurs commonly in waters around all major islands. In the NWHI, distributed from Middle Bank to Kure Atoll in waters from 1 to 77 m.

Distinguishing characteristics

D. VIII, 9; A. 7; LLs. 37. Body rather short, deep, compressed, head rather large, snout long, projecting; mouth slightly oblique, large; maxillary broad at tip; teeth rather large, wide set in a single row in each jaw, none on vomer or palatines; eye small, in posterior half of head; barbels long, reaching nearly to base of ventrals; interorbital space high, convex; opercular spine small, flat; scales large, not firm, edges finely and obscurely ctenoid; lateral line parallel with back, pores not numerously branched (Jordan and Evermann 1905).

Pale rosy red; snout and head smoky red; broad dark red band covering body from eye to origin of spinous dorsal, followed by a pale red band as broad as base of spinous dorsal. A double dark red band extending from the last dorsal spine to the eighth dorsal ray with much black above but scarcely any below the lateral line, followed by a pale band around the anterior end of caudal peduncle, and a dark band around the midregion of the caudal peduncle. Spinous dorsal fin rosy at base, black on distal portion, and a little yellowish in center. Soft dorsal greenish yellow at base, outer three-fourths blackish. Pectorals yellow, rosy on base and in axil; anal fin rosy with cross lines of whitish and anterior border blackish; and caudal dull rosy, edges black (Jordan and Evermann 1905).

Life history

Included among species that occurred in the outer nearshore zone of all the islands in the NWHI surveyed by the HDAR (Okamoto and Kawamoto 1980), the moano is included in this atlas as a representative species of the Family Mullidae which contains many members highly prized in the commercial and recreational fisheries in the Hawaiian Islands.

Moano feeds heavily on crabs and shrimps. At Midway, 95% of the gut content of moano consists of xanthid crabs, mainly *Leptodius exaratus*, and 65% portunid crabs, mostly *Thalamita integra*, and *T. admete* (Sorden 1983). The shrimps include unidentified carideans, alpheids, and *Rhynchocinetes rugulosus*, the latter found only in the moano among several species of goatfish diets studied. Polychaetes including glycerids, *Glycera tesselata*, opheliids, *Armandia intermedia* and *Polyophythalmus pictus*, and two nereid species are other food items in the sample.

Moano occurs over reef and sand pockets either solitarily or in groups of two or three and actively probes cracks and crevices on the reef and pockets of sand with their barbels (Hobson 1974). The species is active through twilight and inactive after dark, but on bright moonlit nights some individuals swim over the reef.

The species spawns at dusk 2 days before the full moon (Lobel 1978). Moano aggregates about a meter above sandy areas 10 m deep next to reefs. The largest fish, presumably the male, is darker than the others and darts conspicuously around and through the aggregation until another fish joins it. The pair then ascends, side by side, spawns while swimming forward just beneath the surface, then descends to the reef.

Gear and catch

Species is taken mainly by trap and handline. In 1961-79, the annual catch fluctuated from 3,206 to 9,528 kg and averaged 5,074 kg. There is no fishery for the species in the NWHI.

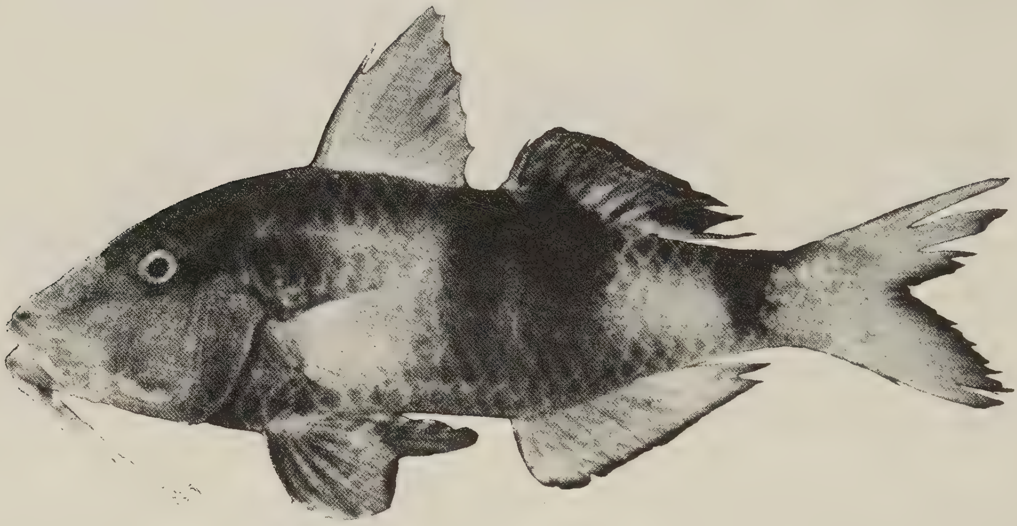

Figure 67.—*Parupeneus multifasciatus*.

86113

by Richard N. Uchida

Valid name	*Panulirus marginatus* (Quoy and Gaimard 1825) (Fig. 42)
Synonymy	*Palinurus marginatus* Quoy and Gaimard 1825; H. Milne Edwards 1837 *Palinurus guttatus* Pfeffer 1881 *Panulirus japonocum* Galtsoff 1933 *Panulirus japonicus marginatus* Chace and Dumont 1949 (from McGinnis 1972)
Common and vernacular names	Hawaiian spiny lobster; lobster; ula

Distribution

Distributed throughout the NWHI from Nihoa to Kure Atoll at depths of 4-174 m.

Distinguishing characteristics

Distinguished from the true lobster by lack of claws and presence of numerous, anteriorly directed spines of varying sizes on the carapace. Anterior dorsal border of carapace with two strong, prominent frontal horns above eyes; two diverging rows of a number of spinules behind the horns. Antennae long, round in cross section, covered with spinules. A pair of strong anterior spines, with several subsidiary spines proximally on antennal plate (anterodorsal surface of the carapace between the antennae). Fifth pereiopods chelate in the female.

Easily distinguished from *P. penicillatus*, the only other species of spiny lobster of commercial importance in Hawaii, by the two pairs of strong anterior spines on the antennal plate (Tinker 1965). *Panulirus penicillatus* occurs very rarely in catches in the NWHI.

Color usually purplish marbled with white but sometimes light yellow, light brown, or dark brown; brownish specimens usually tinted with red (McGinnis 1972). Carapace sometimes pale bluish or greenish behind the cervical groove and pinkish forward (George and Holthuis 1965). Supraorbital horns dark purplish or black with a whitish tip.

Abdominal somites purple with transverse yellow bands along the posterior margins as well as over the transverse groove. Pereiopods almost uniformly dark purple or black. Antennal peduncle pale purplish or pinkish. Telson and uropods purplish at base and bordered posteriorly by a thin yellowish-white stripe.

Life history

Panulirus marginatus is dioecious. Males have the genital orifices on the coxopodites of the fifth pair of pereiopods; whereas the females have orifices on the coxopodites of the third pair. The species is sexually dimorphic. Males are slightly heavier than females at carapace lengths (CL) below 65 mm. At 65 mm CL, males and females have almost identical weights; from about 70 mm CL and larger, females are heavier when compared with males of equivalent length (Uchida, Uchiyama, Tagami, and Shiota 1980).

Lobsters are sexually promiscuous. At Necker Island, females reach maturity at 60.7 mm CL; males at 59.2 mm (Prescott[4]). Males deposit a spermatophore or sperm packet on the sternum of females and a cementing material is extruded around the spermatophore which darkens and hardens (Chittleborough 1976). In NMFS sampling, the smallest female with a sperm packet (mated) was 48.3 mm CL.

Fertilization is external. The Hawaiian spiny lobster is believed to undergo the same ritual during spawning as the western rock lobster, *P. cygnus*. Eggs are extruded from genital orifices and the subchelate dactyls of the fifth pair of pereiopods are used to break the protective coating of the spermatophoric mass. Exposed spermatophores fertilize the eggs which are swept back to adhere to elongated setae on the endopodites of the pleopods. The female is then technically termed ovigerous. The number of eggs extruded is positively correlated with body size (Honda 1980; Honda[5]). The smallest ovigerous female, caught at Necker Island, measured 49.5 mm CL (Uchida and Tagami 1984a).

The spawning season of *P. marginatus* apparently differs within the NWHI chain. Around Nihoa, Necker Island, and French Frigate Shoals, ovigerous females occur mostly in late summer and early winter; toward the northwestern end of the chain, ovigerous females are prevalent in early summer (Uchida, Uchiyama, Tagami, and Shiota 1980). Off Oahu spawning occurs throughout the year and peak activity is concentrated in May-August and low activity is apparent in November-January (McGinnis 1972).

The incubation period lasts about 30 days (McGinnis 1972). After hatching, the phyllosoma larvae float to the surface and become planktonic; the duration of this pelagic phase may be up to 1 year from hatching. Little is known about how larvae are retained around the various islands and atolls of the archipelago. Based on water type oscillations in the Hawaiian region, a hypothesis has been developed to explain the geographic pattern of larval recruitment within the archipelago (MacDonald 1983).

Phyllosoma larvae, which are widely dispersed throughout the chain, pass through 11 dissimilar stages (Johnson 1968). The most advanced stage metamorphoses into a postlarval puerulus (Cooke and MacDonald 1981), a transitional stage between the phyllosoma and the juvenile. A puerulus can swim horizontally allowing it to move shoreward for subsequent settling. Once settled, it assumes the adult coloration.

The NWHI population consists of a single stock (Shaklee and Samollow 1980). There is an excess of males among prehatch embryos. On the assumption that little or no sex-related mortality occurs

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[4] Prescott, J. H. Size at maturity in the Hawaiian spiny lobster, *Panulirus marginatus*, at Oahu and Necker Islands. Fish. Res. Stn., P.O. Box 5, Daru, Western Province, Papua New Guinea (manuscr. in prep.).

[5] Honda, V. A. Fecundity of the spiny lobster, *Panulirus marginatus* (Quoy and Gaimard), in the Northwestern Hawaiian Islands. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396 (manuscr. in prep.)

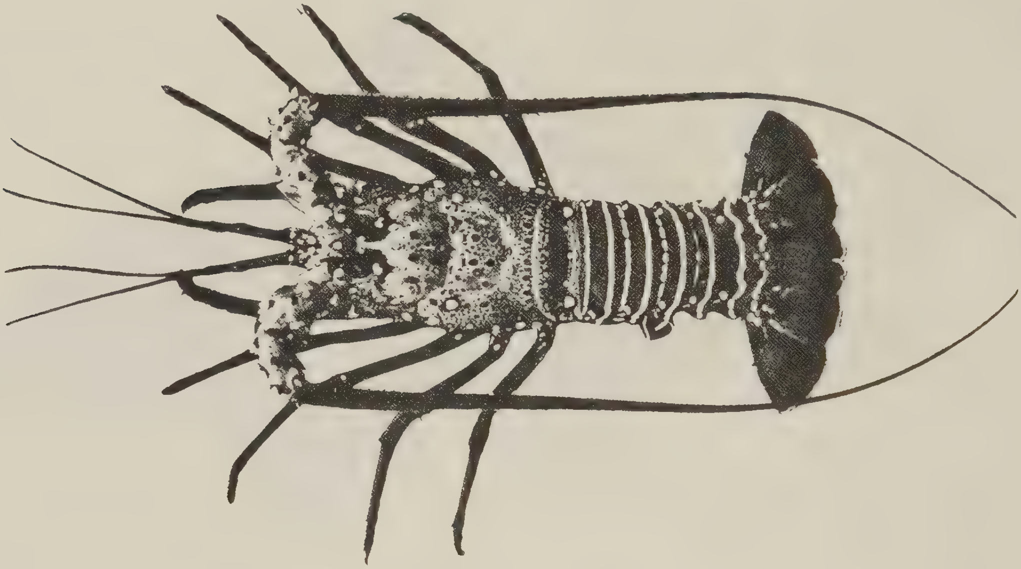

Figure 42.—*Panulirus marginatus.*

from fertilization to the embryo stage, it can be concluded that the sex ratio at fertilization is significantly different from 50:50. The excess of males at the embryonic stage is consistent with the results found in the adult population (Uchida, Uchiyama, Tagami, and Shiota 1980).

Preliminary NMFS study on age and growth for Necker Island lobsters shows that after settling to the bottom, males attain 3.7 cm CL in 1 year, 5.7 cm in 2 years, 7.3 cm in 3 years, 8.5 cm in 4 years, 9.4 cm in 5 years, and 10.1 cm in 6 years. The growth rate of females has not been calculated because of insufficient data. It is believed, however, that growth rates of sexually mature females may be somewhat slower than those of mature males (McGinnis 1972). Data on growth rates from Kure Atoll and French Frigate Shoals (MacDonald 1984) indicate that lobsters from those locations grow slightly faster than those around Necker and Oahu.

Unlike some continental shelf species of Palinuridae that are known to undertake long migrations, insular species like *P. marginatus* make rather short local movements. Tagging studies at Necker indicate that 91% had migrated <9.3 km (5 nmi) when recaptured (Uchida and Tagami 1984a), and a tagging study at Kure Atoll indicated that about 98% had moved <1 km when recaptured (MacDonald 1984). This species occasionally forms queues while moving between locations (MacDonald et al. 1984). Another interesting aspect of the NWHI spiny lobster population is that striking differences occur in average sizes among the various islands and banks surveyed. At Necker, where preexploitation catch rates were the highest in the island chain, the average sizes of males and females were the smallest (Uchida, Uchiyama, Tagami, and Shiota 1980; Uchida and Tagami 1984a).

Gear and catch

The principal gears used in this fishery in the main islands are tangle nets and fish traps. Tangle nets are set mainly for spiny lobsters, and fish traps are primarily used for capturing fish, although lobsters are an incidental catch. In the NWHI fishery, lobster pots of various dimensions and configurations are used.

Until 1976, the spiny lobster catches in the main Hawaiian Islands were small and constituted only a small part of the total marine fish and shellfish landings in the State. During 1961-75, the annual reported catch varied from 1,880 to 5,734 kg and averaged 3,005 kg or <1% of the State's total marine production. Spiny lobsters are also taken in the main islands by recreational fishermen who are not required to report their catches; therefore, the magnitude of the recreational catch is unknown at the present time.

The spiny lobster fishery in the NWHI is relatively new and its short history has been characterized by uneven landings. Populations at Necker Island and Maro Reef, two areas that have commercial concentrations of lobsters, contribute the bulk of the landings in the State. In 1977-82, landings fluctuated between 15,294 (1978) and 354,200 kg per year (1981).

86114

PANDALIDAE — Armed Nylon Shrimp

by Richard N. Uchida

Valid name	*Heterocarpus ensifer* A-Milne Edwards 1881 (Fig. 40)
Synonymy	*Pandalus carinatus* Smith 1882 *Heterocarpus carinatus* Agassiz 1888 *Atlantocaris gigas* Ortmann 1893 *Procletes atlanticus* Lenz and Strunk 1914 *Proclete gigas* Gurney and Lebour 1941 (from Holthuis 1980)
Common and vernacular names	Spot shrimp; armed nylon shrimp; two-spined shrimp

Distribution

Distributed in NWHI from Middle Bank to Kure Atoll at depths of 271-688 m; optimum depth range for trapping the species is 350-599 m (Gooding 1984). Occurs around the main islands most abundantly in depths of 365-440 m (Struhsaker and Aasted 1974).

Distinguishing characteristics

Three carinae (keels or ridges) and an ocellus (eyespot) on either side of the carapace. Postrostral crest and rostrum armed with 16-17 teeth along the dorsal border; 9 teeth along the ventral margin of rostrum. First and second abdominal somites relatively rounded and have no carinae; third and fourth abdominal somites armed with dorsal spines which posteriorly overhang; spine on third somite usually stronger than that on fourth, (although there is some variability in length of spine among non-Hawaiian samples (Hayashi and Miyake 1969)). Carapace translucent and internal anatomy of animal highly visible. Tip of rostrum, anterior portion of carapace, and pereiopods crimson and lighter or pinkish (posteriorly). Ocellus dark crimson and distinct in most specimens. Abdomen uniformly pinkish and ovigerous females carry blue eggs on pleopods.

Life history

The diet of *H. ensifer* includes foraminifers, micromolluscs, and other crustaceans. Forage items found in stomachs are extremely small, usually <0.5 mm. The species is cannibalistic, feeding on body parts, mostly pleopods of other shrimps.

Studies by Clarke (1972), Wilder (1977), and King (1980a, 1980b, 1981) suggested that *H. ensifer* is a protandrous hermaphrodite, that is, initially existing as a male before undergoing sex reversal into a female. Later studies, however, suggest that the species is dioecious and that the sexes can be distinguished by the endopods of the first two abdominal legs (King 1982; King and Moffitt 1984).

Gear and catch

This species is caught in pots of varying design and configuration (Struhsaker and Aasted 1974; Wilder 1979; King 1982; Klemm 1982).

No catch records are available from the fishery, although several boats have operated in the NWHI in the past few years.

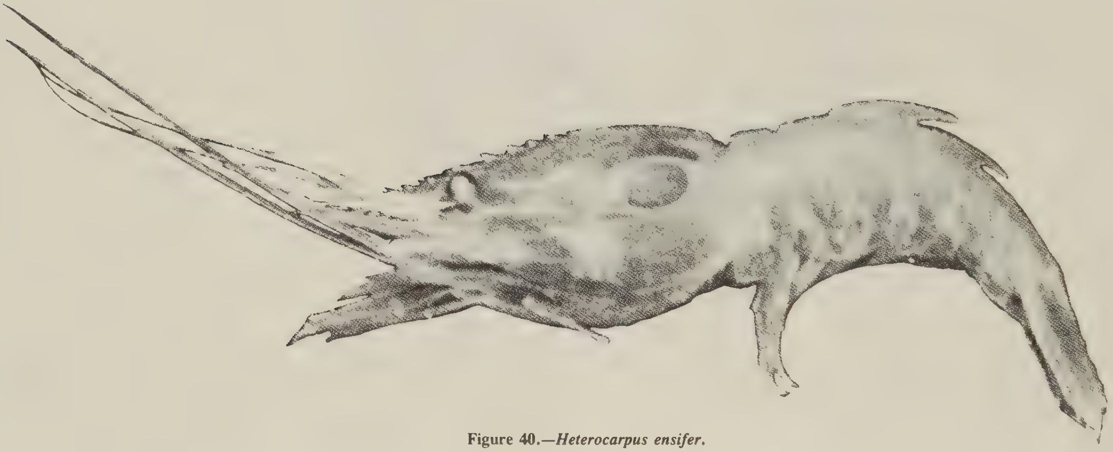

Figure 40.—*Heterocarpus ensifer*.

86115

PANDALIDAE — Smooth Nylon Shrimp

by Richard N. Uchida

Valid name	*Heterocarpus laevigatus* Bate 1888 (Fig. 41)
Synonymy	*Heterocarpus laevigatus occidentalis* Sivertsen and Holthuis 1956 (from Crosnier and Forest 1973)
Common and vernacular names	Smooth nylon shrimp; red-tipped shrimp; ono shrimp

Distribution

Distributed in the NWHI from Middle Bank to Kure Atoll at depths from 497 to 867 m. In most areas, the shallower end of the depth range overlaps that of the deeper end of *H. ensifer*. In the main islands, *H. laevigatus* is most abundant between 440 and 684 m (Struhsaker and Aasted 1974); in the NWHI, the optimum depth range for trapping is 500-799 m (Gooding 1984).

Distinguishing characteristics

Two carinae, but no ocellus on either side of carapace. Postrostral crest and rostrum armed dorsally with 6-7 teeth; ventral margin of rostrum has 10 teeth. Overhanging spines on the abdominal somites lacking; dorsal ridge on third abdominal somite.

Translucent carapace; entire rostrum crimson; orbital region lighter; carapace crimson anteriorly and fading to a lighter shade near the posterior margin. The pereiopods and pleopods crimson, abdomen lighter shade of red. Eggs blue.

Grows much larger (highly desirable commercial characteristic) than *H. ensifer*.

Life history

Male to female sex ratio of 46:54, based on 7,368 smooth nylon shrimp caught in Hawaiian waters departs significantly from equality.[3] Temporal factors rather than geographic ones appear to account for most major population variations in Hawaii. The relationships of sex ratios and sampling depths of smooth nylon shrimp and time of sampling indicate a gradual recruitment of small females from deep (760 m) to shallow (440 m) water, and that adult males and females move between depths of 550 and 700 m in synchrony with the ovigerous cycle of females.

In Hawaiian waters, smooth nylon shrimp spawn primarily in the fall and winter; spawning peaks between October and January. Less than 10% of the females are ovigerous in April-July. Females reach sexual maturity when the carapace length is 40 cm (4-year old). There is no evidence for protandrous hermaphroditism (see footnote 3).

Functional carapace length-weight relations of smooth nylon shrimp in Hawaii were examined separately for males, females without eggs, and females with eggs. These relationships are:

$$\begin{aligned} \text{Males:}\quad & \log_e W = -7.358 + 2.910\,(\log_e CL) \\ \text{Nonovigerous females:}\quad & \log_e W = -6.757 + 2.745\,(\log_e CL) \\ \text{Ovigerous females:}\quad & \log_e W = -5.498 + 2.470\,(\log_e CL) \end{aligned}$$

where W = weight (g) and CL = carapace length (mm). Slopes of the predictive regressions of males, nonovigerous females, and ovigerous females are significantly different (see footnote 3).

Growth rates were estimated by analysis of modal progression of length-frequency distributions. Von Bertalanffy growth equations are:

$$\begin{aligned} \text{Males:}\quad & L_t = 59.7\,(1 - e^{-0.35t}) \\ \text{Females:}\quad & L_t = 62.5\,(1 - e^{-0.25t}) \end{aligned}$$

where L = carapace length (mm) expressed as a function of time t in years. From August 1983 through November 1984 mortality rates were $Z = 1.51\ \text{year}^{-1}$ for males and $Z = 0.73\ \text{year}^{-1}$ for female shrimps. Although male shrimps grow faster than females, they have a substantially higher mortality rate than females (see footnote 3).

Gear and catch

The gear used is identical to that for *H. ensifer* except that the float line (or drop line) must be considerably longer to reach the depths inhabited by this species.

Data on catch are not available, although commercial trapping for this species has begun in the NWHI.

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[3] Dailey, M. D., and S. Ralston. Aspects of the reproductive biology, spatial distribution growth, and mortality of the deepwater caridean shrimp *Heterocarpus laevigatus* in Hawaii. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396 (manuscr. in prep.).

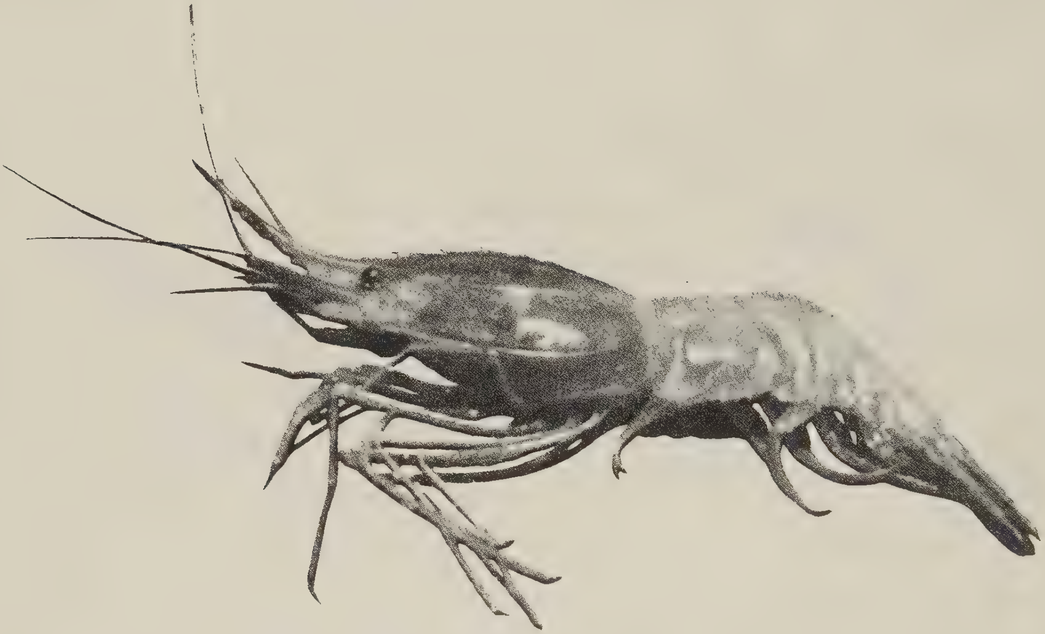

Figure 41.—*Heterocarpus laevigatus.*

86116

PENAEIDAE — Opaelolo

by Richard N. Uchida

Valid name	*Penaeus marginatus* Randall 1840 (Fig. 39)
Synonymy	*Penaeus teraoi* Kubo 1949 *Penaeus* (*Melicertus*) *teraoi* Burukovsky 1972 (from Holthuis 1980)
Common and vernacular names	Royal Hawaiian shrimp; aloha prawn; opae; opaelolo

Distribution

Taken in the NWHI at Laysan (Rathbun 1906), French Frigate Shoals, Necker Island, and Maro Reef at depths of 112-243 m.

Distinguishing characteristics

Small chelae on the first three pereiopods; third pereiopod the longest. Relatively short, sharp-pointed rostrum, reaching a little beyond the tip of the antennular peduncle; armed dorsally with 9-10 teeth; 2-3 teeth on inferior margin. Postrostral crest extending nearly to posterior margin of carapace; bordered on either side by a broad furrow. Dorsomedian carina on abdomen beginning at about one-third the width of fourth somite and extending posteriorly into fifth and sixth somites, ending in acute spine directed posteriorly.

In life, red to pinkish red on dorsal surface and paler on sides; anterior portion of carapace below the eyes and outer edge of tail fan tinged with crimson.

Life history

Almost all members of the Family Penaeidae, with perhaps one or two exceptions, breed in offshore waters. The eggs are broadcast rather than clutched under the abdomen as in most decapods. The hatched larvae are pelagic and usually found far out to sea, although some may be washed into nearshore waters. As growth continues, the larvae are swept into shallow coastal waters where they metamorphose into juveniles. After completing the juvenile phase nearshore, the subadults move offshore into deeper waters. Opaelolo ≤40 mm total length (TL) have been found in nearshore and surface waters between Hawaii and Laysan Island (Rathbun 1906). Larger specimens, 40-95 mm TL, are usually found in harbors and shallow waters; whereas large specimens ≥125 mm are found in waters from 82 to 333 m.

Opaelolo apparently breeds throughout the year (Struhsaker and Yoshida 1975). Around the major islands, opaelolo makes nocturnal movements into shallower depths. Unlike other penaeids, opaelolo shows negative phototactic responses by moving offshore into deeper waters during daytime rather than burrowing. In captivity, however, it burrows readily, indicating that burrowing is also an important behavioral trait.

Gear and catch

Inshore, the species is taken by dip net at night, mostly by recreational fishermen. In deeper waters, for example, in Pailolo Channel, trawls are used. During the existence of a trawl fishery in the Pailolo Channel between 1974 and 1977, catches varied between 2,234 and 4,395 kg per year.

There is no fishery for this species in the NWHI.

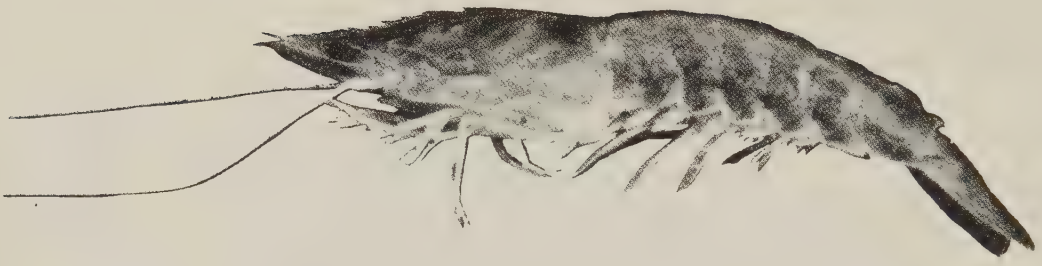

Figure 39.—*Penaeus marginatus.*

86117

PENTACEROTIDAE — Pelagic Armorhead

by Richard N. Uchida

Valid name	*Pseudopentaceros wheeleri* Hardy 1983 (Fig. 68)
Synonymy	*Pseudopentaceros richardsoni* Abe 1957 *Pentaceros richardsoni* Follett and Dempster 1963 *Pseudopentaceros wheeleri* Hardy 1983 (?) *Pseudopentaceros pectoralis* Hardy 1983 (from Hardy 1983)
Common and vernacular names	Pelagic armorhead; armorhead; boarfish; kusakari tsubodai

Distribution

Occurs primarily at Hancock Seamounts in the NWHI at depths of 256-366 m; also at Kure Atoll and Ladd Seamount (its presence at these latter two locations representing a range extension).[19]

Distinguishing characteristics

D. XIII-XIV, 8-9; A. IV, 7-8; P1. 17-18; Gr. 7-8+16-18. Body ovate and compressed; dorsal and anal fin profiles evenly curved; head pointed, encased in exposed striated bones, some of which are rugulose or finely wrinkled. Dorsal spines strong, heterocanth, longitudinally ridged. Generally odd-numbered spines inclined to the left, even-numbered ones to the right. However, this character is not consistent (Abe 1957).

Mouth moderate with cleft slightly oblique; lower jaw projecting forward of upper, with maxilla terminating at anterior edge of a wide irregular area of cheek which is covered with small scutelike scales. Nostrils close together and located slightly closer to the orbital margin than to tip of snout. Lateral line prominent, arching from its origin near the top of the opercle to the base of the fourth and fifth dorsal spines, then running almost parallel to the dorsal outline caudal peduncle and backwards to base of caudal.

Polymorphic; varies from "fat" pelagic type to "lean" seamount type. Morphometric measurements of this species may not be reliable characteristics because of extensive morphological variations, possibly related to spawning (Takahashi and Sasaki 1977; Humphreys et al. 1984; Uchida and Tagami 1984b).

In fresh specimens, upper half of body bluish-gray and paler below. Snout, interorbital, and occipital regions of the head tinged with brown.

Life history

In the central North Pacific, spawning of pelagic armorhead begins from about November-December, peaks in January-February, and declines in March (Takahashi and Sasaki 1977). The free-floating eggs and larvae are dispersed by the North Equatorial Current (Chikuni 1971). By March-April, large numbers of young pelagic armorhead are seen atop the seamounts (Sakiura 1972). The pelagic stage lasts until the juvenile attains 25-30 cm FL and descends to the seamount summits to begin a demersal existence.

The pelagic armorhead, unlike many mesopelagic seamount species, does not confine itself exclusively to the demersal environment throughout its lifetime but also migrates into the epipelagic regime. Catches by Japanese trawlers indicate the fish at depths between 300 and 600 m over the central North Pacific seamounts. Other reports indicate that pelagic armorhead is caught in salmon gill nets or with handline near the surface. The species has also been found in stomachs of surface feeding sei whales. This points to the possibility of extensive vertical migration by the species.

Investigators disagree on time of vertical movement. Some report that pelagic armorhead rises to the surface at night, feeding on organisms such as euphausids, mysids, copepods, salps, shrimps, and myctophids which are usually associated with the deep-scattering layer that ascends toward the surface at night (Hart 1973; Sasaki 1973). Others report that armorhead rises to the surface during the day and descends to the summits at night (Sakiura 1972; Kuroiwa 1973). The NMFS bottom trawl catches were better at night than day indicating that the species was associated with the seamount summit at night.

The fork lengths of unsexed armorhead taken by trawling on NMFS cruises show strong unimodal distributions. At NW Hancock fish ranges between 233 and 398 mm FL and averages 297 mm; 67% of the fish falls between 290 and 310 mm. At SE Hancock, the fish does not appear to differ in size from those at NW Hancock. It ranges from 233 to 359 mm and averages 299 mm, and about 62% of the fish falls within 290 and 310 mm. Females are significantly larger than males (Humphreys et al. 1984). Japanese data indicate that the size of armorhead taken from all the central North Pacific seamounts tended to decrease from 1969 to 1972, then to increase from 1973 to 1976. In all years studied, the size range was narrow. Other studies confirm that no significant differences in fish size occur among the seamounts (Sakiura 1972; Iguchi 1973; Sasaki 1974; Aomori Prefectural Fisheries Experimental Station 1976).

Annual marks are found on the sagittae (otoliths), centrum of vertebrae, and spines of the dorsal, pelvic, and anal fins. Annuli counts are consistent among these hard parts. Preliminary length-age relationships of the pelagic armorhead caught at Hancock Seamounts are 28.8 cm for males and 30.4 cm for females at 2 years and 29.5 cm for males and 31.0 cm for females at 3 years. A few age determinations made by enumerating daily increments on the sagittae are in agreement with ages estimated by annuli.[20] However, both methods used to estimate age of the pelagic armorhead have

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[19] Tagami, D. T., Research Assistant, Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, pers. commun. August 1983.

[20] Uchiyama, J. H., and J. D. Sampaga. Age and growth estimates of the pelagic armorhead, *Pentaceros richardsoni*. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396 (manuscr. in prep.).

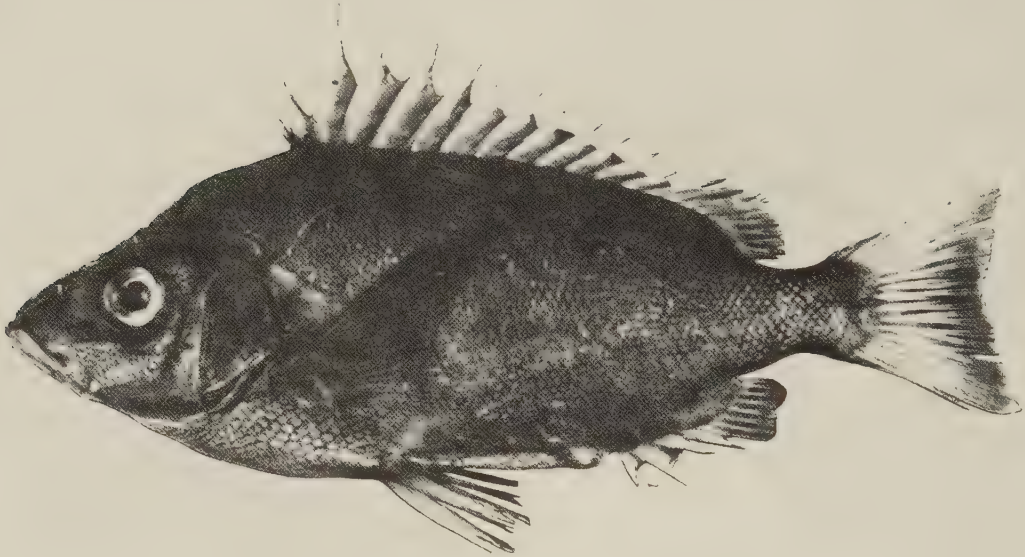

Figure 68.—*Pseudopentaceros wheeleri.*

not been validated. Another aging study using scales estimates that a 22-cm pelagic armorhead is 3 years old and a 32-cm fish is 6 years old (Chikuni 1970).

Gear and catch

Pelagic armorhead is taken mainly with bottom trawl, although small numbers are also taken by handline gear. Traps apparently are ineffective (Uchida and Tagami 1984b).

Catch data, available from the Japanese trawl fishery, showed that at Hancock Seamounts, the annual catch in 1969-81 varied between 67 and 8,518 MT and averaged 1,234 MT. Since 1977 when the MFCMA went into effect, however, annual catches have not exceeded 739 MT. Annual catches from the remaining seamounts in the central North Pacific varied from 433 to 32,794 MT and averaged 12,928 MT in 1969-81.

86118

PRIACANTHIDAE — Glasseye Snapper

by Richard N. Uchida

Valid name	*Priacanthus cruentatus* (Lacepède 1802) (Fig. 50)
Synonymy	*Labrus cruentatus* Lacepède 1802 *Priacanthus carolinus* Lesson 1826 *Priacanthus macrophthalmus* Cuvier and Valenciennes 1829 *Priacanthus boops* Cuvier and Valenciennes 1829 *Priacanthus blochii* Günther 1851 (?) *Priacanthus schlegelii* Hilgendorf 1879 (from Weber and De Beaufort 1929)
Common and vernacular names	Glasseye snapper, red bigeye, aweoweo

Distribution

Occurs throughout the main islands. In the NWHI, they occurred from Necker to Midway at depths from 20 to 296 m.

Distinguishing characteristics

D. X, 13; A. II, 14; LLs. 11-100-53 (Jordan and Evermann 1905). Body moderately elongate, deep, laterally compressed, covered with small, rough ctenoid scales; dorsal and ventral outlines similarly curved; snout bluntly pointed; lower jaw prominent, strong, and projecting; mouth moderate, oblique; lateral line runs dorsally to area of caudal fin base then descends to midlateral caudal peduncle (Jordan and Evermann 1905; Schultz et al. 1953).

Teeth small, villiform on jaws, vomer, and palatines; gill rakers long, slender; tongue broad, rounded and free; maxillary extends to anterior edge of pupil; eyes large; fins moderate with origin of spinous dorsal over upper base of pectoral; dorsal spines short, stout, blunt; soft dorsal rounded; caudal truncate; pectoral short, broad; preopercle strongly toothed with a strong rugose toothed sharp or blunt variable spine at angle (Jordan and Evermann 1905; Schultz et al. 1953).

Bright red mottled with silvery white in life; six dark red vertical bars alternating with fainter bars on side of back; dorsal and caudal fins rosy; iris and jaws deep red.

Life history

Glasseye snapper are nocturnal predators, feeding on free swimming organisms (mostly crustaceans and cephalopods), and inhabiting reefs, bays, and harbors (Hobson 1974). Fishes and polychaetes make up the bulk of the remaining food items (Randall 1967). A study conducted off Kona, Hawaii demonstrated that the species takes shelter in groups or singly under rocks or coral during daylight (Hobson 1974). At night, they emerge from the shelter, assemble in schools high in the water column, migrate offshore, and do not return to the reef until about 40 minutes before sunrise. Lesser numbers, mostly solitary or in small groups, remain over inshore reefs throughout the night. All fish were noted to return to daytime shelter 30 min before sunrise.

Gear and catch

Glasseye snapper is caught around the main islands primarily with handline and gill net.

The State annual landings of this species fluctuated between 780 and 4,764 kg, averaging 1,886 kg during the period 1961-69.

There is no fishery for priacanthids in the NWHI.

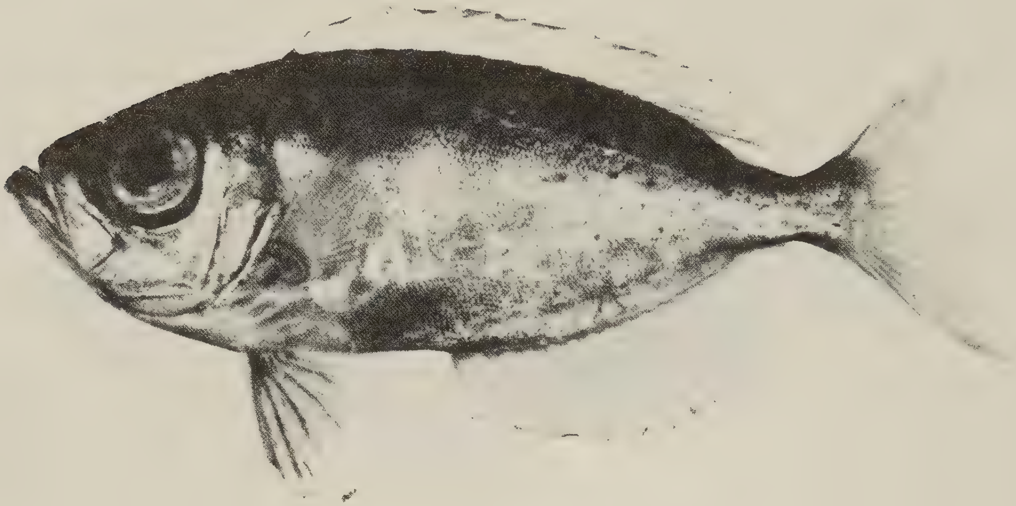

Figure 50.—*Priacanthus cruentatus.*

86119

RANINIDAE — Kona crab

by Richard N. Uchida

Valid name	*Ranina ranina* (Linnaeus 1758) (Fig. 45)
Synonymy	*Cancer raninus* Linnaeus 1758 *Ranina dentata* De Haan 1841 *Ranina serrata* Lamarck 1892 *Ranina scabra* Fabricius 1918 (from Sakai 1937)
Common and vernacular names	Red frog crab; frog crab; spanner crab; kona crab; papaikualoa

Distribution

Distributed in the NWHI from Nihoa (Edmondson 1946) to Kure Atoll at depths from 24 to 115 m; also found in the main Hawaiian Islands.

Distinguishing characteristics

Carapace broad anteriorly, narrow posteriorly, strongly convex from side to side, and covered with numerous small rounded spines; anterolateral margins of carapace armed with dorsoventrally compressed sharp spines which occur either singly or in sets of three or four on protruding processes; anterolateral processes small in young of both sexes, but become prominent in large adult males.

Dioecious and sexually dimorphic. Seven segments forming abdomen relatively narrower in the male than in a female of similar size. Male grows larger, has larger chelae; setae on the palmar surface of dactyli and propoda of chelae, genital openings on coxae of fifth pair of pereiopods; larger, anterolateral carapace spines, giving carapace a square look (Onizuka 1972; Fielding and Haley 1976). Female has well-developed pleopods with numerous setae, oviducts that open on the coxae of third pair of pereiopods, and in mature individuals an external, medially located spermatheca on the seventh sternite between the third and fourth pairs of pereiopods (Gordon 1963).

Broad, flat chelae strong, equal in size, dorsal surface covered with small rounded spines similar to those found on carapace. Two sharp spines along the outer margin and five on the inner margin of flattened propodus. Remaining pereiopods expanded, paddle-shaped dactyli. Abdomen not completely folded under cephalothorax so that at least four to five segments exposed in dorsal view.

Color along dorsal surface usually deep orange but some may be bluish. Immature individuals may be white (Fielding and Haley 1976). The ventral surface white.

Life history

There are two separate studies on the reproduction of kona crab in the main islands. At Penguin Bank, the smallest mature male found was 43.6 mm CL, whereas, the smallest mature female was 54.3 mm CL (Fielding 1974). Mature individuals, however, may not necessarily be reproductively active. Off Oahu's north shore, females first became ovigerous at 63 mm CL (Onizuka 1972). Females smaller than 58 mm CL lacked developing ovaries. Among those averaging 60 mm CL (58-62 mm), 83% were mature whereas at 65 mm CL (63-67 mm), about 87% were mature. At Penguin Bank, 50% of the females in the 70-76 mm size group were reproductively active (Fielding 1974). Among males, all crabs ⩾60 mm CL had mature spermatozoa (Fielding and Haley 1976), but the exact size at which males copulate has not been determined.

Fertilization is external. Although no observations on fertilization have been made, it is believed that it is accomplished as the eggs pass the spermatheca (Onizuka 1972). The fertilized eggs are then swept back and adhere to the numerous elongated setae on the pleopods.

Around the main islands, ovigerous females occur in the catch only from May through September (Onizuka 1972; Fielding and Haley 1976). Data collected in the NWHI were insufficient to define the spawning season; however, at Maro Reef ovigerous females were collected in July and none in January.

Kona crabs spawn at least twice per season. The spherical eggs, which are orange when newly spawned, become brown when the eyed stage is reached in about 24 days and hatch 5 days later (Onizuka 1972). Females usually spawn a second batch of eggs about 9 days after the first spawns are hatched.

At the start of the spawning season in May, the number of eggs produced is positively correlated with carapace length (Fielding and Haley 1976). A 63-mm CL female can spawn an estimated 27,000 eggs; whereas, a 114-mm CL female can produce more than 145,000 eggs at a time (Onizuka 1972). At the end of the spawning season, however, the number of eggs produced apparently is unrelated to body size (Fielding and Haley 1976). The number of eggs produced also varies from season to season.

Little is known about the planktonic dispersal stages of kona crabs. The first molt occurs 7-8 days after hatching and the second molt occurs about 7 days later (Fielding and Haley 1976).

The species is carnivorous and apparently feeds at any time of the day (Onizuka 1972). The crab lies buried in the sand with only a few millimeters of the anterior portion of the carapace and eyes protruding above the sand, waiting for prey or food particles.

At sizes <40 mm CL, the increase in carapace length during each molt is about the same for both sexes; however, at larger sizes, the female growth rate is slower than males (Onizuka 1972). Molting frequency and growth increment also decrease with age. Furthermore, it has been reported that in January and March, a large percentage of the females bear new shells. This indicates recent molting and suggests that most females molt at least once during the early months of the year before the onset of the spawning season. The males, on the other hand, have a protracted molting period beginning in January and lasting through August. It is estimated that a 5-year-old male is 10.2 cm CL; a female of the same age averages about 8.9 cm ([Hawaii] 1970).

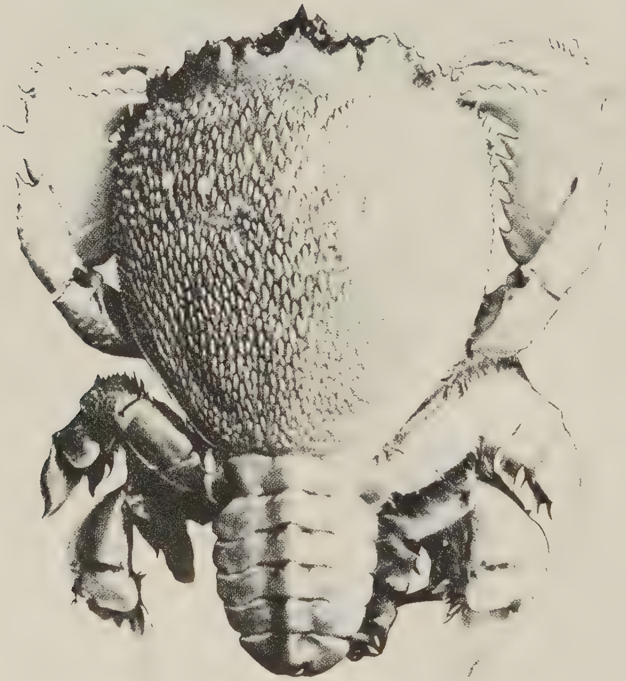

Figure 45.—Female *Ranina ranina.*

The male to female sex ratio deviates significantly from 50:50 (Onizuka 1972; Fielding and Haley 1976). At Oahu and Penguin Bank, stocks are roughly 55% males and 45% females. In the NWHI, male to female ratios were 66:34 at French Frigate Shoals, 62:38 at Maro Reef, and 75:25 at Pearl and Hermes Reef. Samples from elsewhere in the NWHI were too small to derive meaningful sex ratios.

Kona crab caught in the NWHI ranged from 70 to 167 mm CL. Carapace width-weight relationships of 501 males and 254 females were:

$$\text{Male:}\quad W = 5.689 \times 10^{-4}\ CW^{2.9478}$$
$$\text{Female:}\quad W = 7.719 \times 10^{-4}\ CW^{2.8070}$$

where W = weight (kg) and CW = carapace width (cm).

Gear and catch

There is a small fishery for kona crab in the main islands. The principal gear used is the kona crab net, although one vessel fishing in NWHI waters has successfully used crab traps. Commercial vessels usually set, haul, and reset the strings of nets several times during the day from sunrise to sunset. Soaking time, usually 1 h, is necessarily kept short because longer soaking attracts predators such as sharks and rays which can inflict extensive damage by tearing off the bait and entangled crabs from the netting.

During 1961-79, the annual catches of kona crab around the main islands fluctuated between 4,215 and 32,835 kg and averaged 13,519 kg.

At present, there is no fishery for kona crab in the NWHI. Two boats previously fished for kona crab experimentally in the NWHI, but have since quit fishing.

86120

SCYLLARIDAE — Ulapapa

by Richard N. Uchida

Valid Names	*Scyllarides squammosus* (H. Milne-Edwards 1837) (Fig. 43) and *S. haanii* (De Haan 1841) (Fig. 44)
Synonymy	(for *Scyllarides squammosus*) *Scyllarus squammosus* H. Milne-Edwards 1837 *Scyllarides squamosus* Holthuis 1946 (for *Scyllarides haanii)* *Scyllarus haanii* De Haan 1841 *Scyllarides haanii* Holthuis 1946 (from George and Griffin 1973)
Common and vernacular names	Slipper lobster; shovel-nosed lobster; scaly slipper lobster; sea crawfish; Spanish lobster; ulapapa

Distribution

Widely distributed in the NWHI from Middle Bank to Kure Atoll. The NMFS catch data indicate that *Scyllarides squammosus* is distributed at depths from 13 to 137 m, and *S. haanii* is distributed from 33 to 112 m.

Distinguishing characteristics

Scyllarides squammosus—Carapace slightly longer than broad, widest near the posterior margin; surface of carapace and terga granulate; granules low, smooth, and each surrounded by numerous small, fine, stiff setae; anterolateral corner of carapace only slightly wider than width at cervical groove, which is weakly defined; anterolateral margin forms an obtuse angle with anterior margin of carapace; entire lateral margin of carapace armed with small, blunt anteriorly directed spines, those anterior of the cervical groove slightly larger; gastric area of carapace elevated with the cardiac and branchial regions only weakly elevated; four anteriorly directed weak spines on supraorbital region of carapace; posterior transverse groove deep, prominent.

Antennae large, flat, distal segment rounded, the leading edge finely serrated; minute fine, short setae on upper surface penultimate segment small bearing two weak spines directed forward along the inner margin; second segment largest, broad, flat, and coarsely granulate, lateral margin slightly convex, and one weak spine at juncture of the anterior and lateral margins, which form an obtuse angle; inner margin of second segment also armed with two anteriorly directed spines; leading edge of second segment more strongly serrated than distal segment; a coarsely granulated proximal segment extending from outer edge of eye socket to center line in front of rostrum dorsally subtriangular; three spines on inner leading margin of proximal segment; two additional spines at center of distal margin, and a cluster of four spines at the outer distal margin.

First segment of abdomen short, narrow, and usually partially under the carapace; weak ridge along the middorsal line of second, third, and fourth segments; appearing as weak humps when viewed from the side. Sternum deeply emarginate; weak, blunt protuberances on lateral end near juncture with the pereiopods.

Scyllarides haanii—*Scyllarides haanii* and *S. squammosus* are morphologically similar and can be confused easily. Differences are: Dorsal carinae of carpus of first and second pereiopods low in *S. haanii* but distinct in *S. squammosus* (George and Griffin 1973). Carapace of *S. haanii* broader and more deeply emarginate along the anterior ventral margin of the carapace. Dorsal midline of abdominal segments 3 and 4 is strongly elevated or humped in *S. haanii* but only a weak ridge in *S. squammosus* (Morin and MacDonald 1984).

Life history

Female *Scyllarides* have never been observed with attached spermatophores or remnants of a spermatophoric mass, suggesting that fertilization is internal (Lyons 1970). Among 1,090 females collected throughout the chain from our NWHI cruises, none had a spermatophoric mass although 33% of the females examined were ovigerous.

Like spiny lobsters (see Uchida, Uchiyama, Humphreys, and Tagami 1980), catches of slipper lobsters during this study varied widely throughout the NWHI. Our data show that catch rates of slipper lobsters were relatively higher at Brooks Banks, Gardner Pinnacles, Maro Reef, Northampton Seamounts, Lisianski Island, and Pearl and Hermes Reef. Contrary to results of trapping at Lisianski where spiny lobsters were not abundant, slipper lobsters occurred in good numbers at this location. The highest catch rates occurred at depths between 20 and 55 m.

Slipper lobsters predominated over spiny lobsters in the catches at Brooks Banks (77%), Northampton Seamounts (89%), Lisianski Island (93%), and Salmon Bank (82%). Overall, however, the percentage of slipper lobsters in the catch throughout the NWHI was only 16%.

The sex ratio of slipper lobsters showed an interesting pattern. Whereas the male to female ratio was near 50:50 or in favor of females at the lower end of the NWHI chain from Middle Bank to St. Rogatien Bank, it was heavily in favor of males at Brooks Banks and northward from Gardner Pinnacles to Kure Atoll. Data combined for all areas showed a sex ratio of 56:44 (males to females).

The proportion of the various sizes of slipper lobsters in the catch also showed abrupt changes in the NWHI. Carapace length-frequency distributions of slipper lobsters taken from Middle Bank to Salmon Bank showed a large proportion of the catch (77%) was made up of lobsters 7.8-10.2 cm; most of the remainder (19%) were in the 5.3-7.7 cm range. In the northern end of the chain, Pearl and Hermes Reef, Midway, and Kure Atoll, however, small, medium, and large lobsters were equally represented; 29% in the 5.3-7.7 cm group, 26% in the 7.8-10.2 cm group, 21% in the 10.3-12.7 cm group, and 22% in the 12.8-15.2 cm group. The remaining 2% of the catch were lobsters >15.3 cm CL.

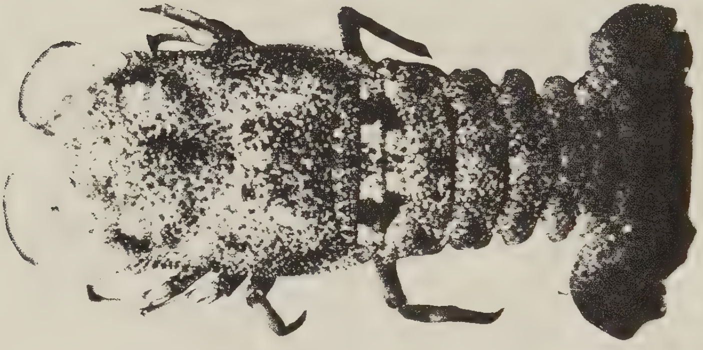

Figure 43.—*Scyllarides squammosus.*

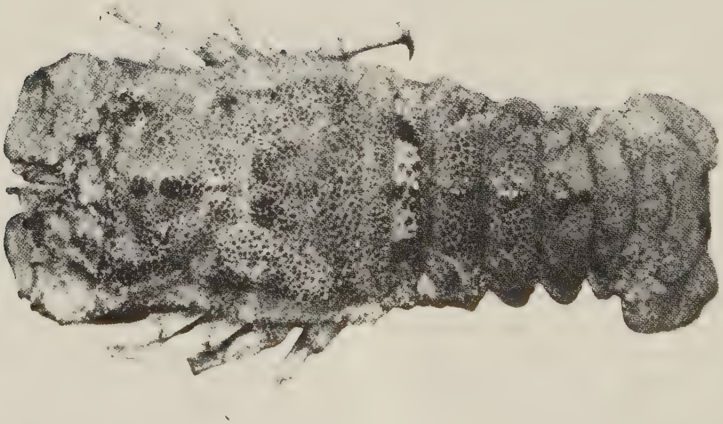

Figure 44.—*Scyllarides haanii.*

Gear and catch

Slipper lobsters are usually taken incidentally while trapping for spiny lobsters. During 1961-75 (1976-78 catches not given in HDAR annual catch reports), annual reported catches of slipper lobsters ranged from 2 to 126 kg and averaged only 33 kg; however, since the beginning of the NWHI spiny lobster fishery, incidental catches of slipper lobsters have risen. In 1979, the reported catch of slipper lobsters reached 344 kg, presumably almost all of which came from the NWHI.

86121

Session 1. Summary

RICHARD N. UCHIDA and SIGEITI HAYASI

Two papers were presented during the session. The first by Roden dealt primarily with the effects that seamounts have on the ocean's thermohaline structure and generated an active exchange of opinions during the discussion. The behavior of this structure and the circulation depend on several factors including speed and sheer of the oncoming flow, shape and orientation of the seamount, vertical stratification, and rotation of the earth. When conditions are favorable, stationary water masses called Taylor columns may form near seamount peaks, whereas under other conditions eddies may be shed from the seamount. Not all Taylor columns reach the sea surface. Those that do are more easily observed in winter by their low temperatures; in summer, the temperature contrast is minimal at the sea surface because the Taylor column may not extend above the mixed layer. The duration and frequency with which Taylor columns form have not been researched.

Yamanaka presented the second paper which reviewed results of investigations into the association of fish schools with oceanographic conditions in the vicinity of seamounts and other undersea features. He cited studies which showed that size and shape of seamounts, depth of the summit, bottom topography, water quality, and current strength all contribute to the formation of eddies and upwelling which aggregate fish. In these eddies, water color and transparency change and productivity is high near the summit. Many phenomena in the vicinity of seamounts need to be clarified. For example, one study showed that tuna usually aggregated upstream of seamount eddies whereas prey were found downstream. Unique bottom conditions around Crozet and Kerguelen Islands have been reported to be responsible for accumulating Antarctic krill and whales. Undersea ridges, which alter surface circulation, have influenced the transport and dispersion of fish eggs and larvae.

Yamanaka reported that even artificial reefs, although small compared with seamounts, also influence currents, to some extent, and may serve as models in the study of circulation over and around seamounts.

In the discussion that followed, Roden emphasized that to properly investigate the influence of seamounts on the oceanic environment, three-dimensional sampling would be required. Sampling stations should be spaced not more than 20 km apart for large seamounts and 5 km apart for small ones. Combination of ship, satellite, and satellite-tracked drifter measurements should produce results superior to single measurements. Accurate navigation and precision depth recording are also essential, and hydrographic stations should be conducted to depths of 3,000 m and preferably to the bottom.

Discussion also brought out that the height of the Taylor column is associated with the strength of the vertical stratification, that is, the stronger the stratification, the shorter the column. Furthermore, whether a Taylor column can be detected on the sea surface depends on weather conditions. Differences in water color and transparency can be seen over, and adjacent to, seamounts to some extent. On cyclonic and anticyclonic eddies in the vicinity of seamounts, the discussion centered on Yamato Bank located at the division of two current systems. Observations at this bank showed current speed in the southern part of the bank was twice as fast as that in the northern sector.

On a question of whether information on topography and other parameters could be used to develop models for other seamounts, Roden replied that a generalized model will be quite difficult to construct, explaining that some models will provide answers some of the time, but no generalized model is possible for all seamounts.

Another point brought up was the depth profile of chlorophyll *a* in the vicinity of seamounts. Yamanaka responded that because his presentation was an overview of other investigations, he was not able to describe its depth distribution. The question of why aggregations of small fish appear on the downstream side and large fish such as tunas occur on the upstream side was brought up but remained unanswered for lack of research information.

86122

Session 2. Review of Seamount Fisheries

RICHARD N. UCHIDA and SIGEITI HAYASI

This session was devoted to a review and discussion of the present status of seamount fisheries.

Sasaki traced the historical development and described the present status of the Japanese trawl fishery for pelagic armorhead and alfonsin over the seamounts of the southern Emperor-northern Hawaiian Ridge. Of particular significance was the drastic decline in catches of pelagic armorhead beginning in 1976. Whereas pelagic armorhead represented more than 90% of the total trawl catch in 1969-75, they constituted only 80% in 1976, 59% in 1977, 26% in 1978, and between 5 and 13% since then. The alfonsin catch, however, has risen, reaching 87% of the trawl catch in 1982.

Sasaki concluded that the rapid decline in relative abundance of pelagic armorhead in 1973 and subsequent years was a reflection of reduced stock size and recruitment resulting from overexploitation in 1967-75. He reported that for alfonsin, relative abundance remained high at Kimmei and Milwaukee Seamounts, declined at Colahan Seamount, and was generally low at Hancock Seamounts.

Sasaki emphasized that open-ocean seamounts are not highly productive and resources associated with them cannot support large trawl fisheries. The exceptions were the seamounts in the southern Emperor-northern Hawaiian Ridge; however, highly efficient trawling operations can easily deplete the resources because of the limited habitat.

Seki and Tagami traced the historical development of the handline and bottom longline fisheries for alfonsin. Since the fishery began in 1875, it has expanded and now includes the grounds off Chiba Prefecture and Shimoda to those in distant waters near Nansei Islands and Zunan. Fishing grounds developed as far away as Midway, however, have been abandoned in recent years.

Current NMFS research on alfonsin has been concentrated in the southern Emperor-northern Hawaiian Ridge seamounts and has emphasized the Hancock Seamounts. Handline and vertical longline catches from untrawlable and sloping areas of the seamounts, indicated that although the size of pelagic armorhead taken by handline and by trawls were nearly identical, alfonsin taken by handline were significantly larger than trawl-caught ones.

Yasui's presentation brought out that the albacore, although highly migratory, apparently were associated with seamounts in the Emperor Seamount chain during one phase of their transpacific migration. Catches in the region of the seamounts ranged from 4,000 to 15,000 MT, comprising 5 to 25% of the total albacore landings by Japanese vessels. By following fleet movement, Yasui determined that albacore first appeared near the seamount chain at Kimmei, then moved northward along the chain and finally westward. The albacore taken here were usually 2- to 5-year olds, although certain age groups were absent in some years. The albacore apparently remained relatively long in the seamount region, feeding mainly on sardines and squids.

In the discussion that followed, it was brought out that because catches of pelagic armorhead over the central North Pacific seamounts fluctuate considerably, it may be appropriate to consider the species pelagic rather than demersal. Studies of other species indicated that, in general, pelagic stocks undergo wider fluctuations in abundance than demersal ones. It was noted that at times, it is difficult to differentiate pelagic from demersal stocks and that pelagic armorhead should really be considered a demersal species because over the past 3-4 years, there has been no improvement in the catch.

An example of reduction in CPUE in two contrasting fisheries involved a local groundfish stock in which reduction in CPUE was fishery-dependent and in a highly migratory pelagic stock in which the reduction was fishery-independent and brought about by changes in oceanic conditions. It was noted that even groundfish can sometimes exhibit large natural fluctuations during their early pelagic stages.

The following explanations appear to be reasonable for two of the papers presented in this session. For albacore, it does not appear that the CPUE around the seamounts is representative of the entire stock, because the species is widely distributed and migrates extensively over a wide range and only some portion of the stock visits the Emperor Seamounts. For pelagic armorhead, however, the continuous reduction of CPUE can be considered a decrease in stock size, because the species only inhabits waters around certain seamounts.

For alfonsin, it was pointed out that the reduction of CPUE could be only a temporary phenomenon because of its migratory habits. The possibility that the reduction in alfonsin CPUE could reflect the practice of discarding small fish was also raised, but it was brought out that there is no evidence that this was occurring.

A question of whether the increase in total catch of alfonsin was directly related to a decrease in the stock of pelagic armorhead brought out that the trawlers began targeting alfonsin when pelagic armorhead fishing was no longer profitable. On this same line of questioning, Sasaki was asked if any significant adjustments were made to trawling operations in targeting the alfonsin. He replied that none was required except in fishing depth. He added, however, that in trawling for pelagic armorhead, the net was towed directly off the bottom except where large populations of pelagic armorhead were detected. When this occurred, the trawl was fished higher in the water column. Similarly, trawling for alfonsin required only a depth adjustment to fish higher off the bottom.

Pelagic armorhead and alfonsin occurred in good quantities over the seamounts but early commercial trawling operations only targeted the former because of economic reasons. Their abundance over the seamounts was so high that large trawlers could easily make profitable catches. In addition, because alfonsin was sold fresh in Japanese fish markets, frozen ones were not considered highly desirable. It was brought out that freezing clouded the eye lenses of alfonsin making them lower in value. It was noted that alfonsin occurred in good numbers only on two seamounts in the southern Emperor-northern Hawaiian Ridge whereas pelagic armorhead were abundant at four of the seamounts.

Before the session concluded, participants expressed concern on whether increased catches of alfonsin truly reflected an increase in abundance of the species, in view of the decrease in the stock of pelagic armorhead. It was brought out that more studies were needed on ecological factors that influence the stock, on depth distribution of the two major seamount-associated species, and on composition of the seamount community.

86123

Session 3. Summary

RICHARD N. UCHIDA and SIGEITI HAYASI

The two papers presented in the session demonstrated that other important and potentially important resources are associated with seamounts. In the first paper, Grigg reported that precious corals may be found in the vicinity of seamounts and that the precious coral fishery can be considered in part a seamount fishery.

Commercial grades of precious coral are red and pink (*Corallium* spp.). Less valuable corals include gold, black, and bamboo. In the last 5 years, more than half of the world's supply of *Corallium* sp. has been harvested from grounds in the Emperor Seamounts at depths between 400 and 1,500 m. Recent discoveries of new precious coral grounds in the Mediterranean and off Hokkaido are also associated with seamounts or shallow banks.

In the second paper Alton dealt with fish and crab populations associated with Gulf of Alaska seamounts. These seamount populations were composed mainly of commercially valuable species that are part of the lower slope community of the continental shelves in the northeastern Pacific. Alton, however, found no evidence of recruitment of young fish to the seamount populations, that seamount-associated sablefish were large, mature fish that arrived from other regions, and that there was a low rate of emigration from the seamount populations.

Alton concluded from the surveys that despite high catches of crabs and sablefish from seamounts, the nature of the population and the limited habitat suggest that seamount populations can support only a limited fishery.

Discussion on the presentations brought out that coral tangle nets are about 40% efficient. Repeated passes of this type of gear break up coral and cause extensive damage to the grounds, which may require many years to recover.

In response to a question of aging coral, Grigg replied that growth rings can be used to determine age of mature coral. He noted that gonadal development may slow coral growth and thus ring formation. Immature coral, however, also shows evidence of growth rings, but it is not known why they occur. Grigg stated that for some species, male coral matures at age 2 and females at age 4.

Coral harvesting can also be done by the use of submersibles, but whether it is efficient to do so depends on economic considerations.

On a question of how mature sablefish find their way from their lower-slope habitat to the offshore seamounts, Alton speculated that sablefish migrate in midwater to reach them. The rationale for such speculation is that the seamount-associated sablefish are firm-fleshed, unlike some continental slope sablefish which inhabit deep water and have softer flesh. Furthermore, sablefish have been reported in catches of midwater trawls.

For hake caught by trawling over Alaskan seamounts, it was noted that they differed in size and age from those taken by trap fishermen off Oregon, indicating differential growth rates by area. Sablefish from the eastern Bering Sea as well as over the seamounts showed extensive horizontal and vertical distributions; therefore, even if the seamount stock of this species were harvested intensively, the effect of fishing would not be as severe as that for pelagic armorhead, which is closely associated with and dependent on the seamount habitat.

Further discussion pointed out that the sablefish resource in the North Pacific is not limiting, and the present fishing intensity is not likely to affect it. Any fishery developed for the seamount-associated sablefish, however, would need to be properly managed.

86124

Session 4. Summary

RICHARD N. UCHIDA and SIGEITI HAYASI

Three papers were presented in this session. The first, by Humphreys on pelagic armorhead, reviewed geographic and depth distributions, diurnal migration, food and feeding habits, and spawning, and discussed existing controversy surrounding age and growth, morphological variation, and systematics. The paper also provided a life history to account for the existence of different body types and reproductive conditions.

The second paper by Koami discussed the necessity of obtaining detailed topographic information on submerged banks and seamounts for efficient and long-term utilization of the marine resources associated with them. Detailed topographic information provides clues to finding productive fishing grounds for particular species. To prevent overfishing and eventual collapse of a fishery, Koami advocated establishment of a rotational system much like that used to reforest deforested areas. On a local scale, prefectural governments should cooperate to establish a system whereby species are harvested on a rotational system. The system, according to Koami, can also be applied to fishery resources of the North Pacific, but agreement will have to be reached amongst all nations harvesting the resource.

The third paper was presented by Fujii, who examined species composition of fish fauna over seamounts, seamount chain, ridges, banks, tablemounts, and continental slope. Classifying the fish fauna as ''shelf,'' ''oceanic,'' and ''deep-sea,'' Fujii reported that seamount-associated fish fauna is influenced by characteristics of the surrounding water mass. For example, tropical and temperate water species are not mixed except at watermass boundaries, and a seamount with an overlying layer of low-oxygenated water has a fish fauna low in species diversity as well as biomass.

The ichthyofauna of seamounts is not as limited as believed. Fujii said that seamount shape influences community composition and density. Seamounts with narrow summits have fish communities of low species diversity and density compared to those found over continental slopes. The number of species, however, increases with the area of the summit. Tablemounts, for example, have communities with species diversity about equal to, and density higher, than those found over some continental shelves.

Because endemism is found only among bottom dwellers, Fujii pointed out that many endemic species are known from various seamounts, thus indicating isolation; therefore, seamounts may have important roles in speciation of fishes. He discussed speciation in the Pentacerotidae in some detail.

The discussion during the session brought out that studies on seabird diet and feeding behavior show no seamount-associated species among the prey items. A question was raised on the pelagic armorhead's life history, whether ''fat'' fish, which eventually mature and change morphologically to ''lean'' fish, will recover sufficiently to become ''fat'' once again. Humphreys replied that no concrete evidence of this type of change is available; however, in his opinion, ''lean'' fish will probably never recover and perish after spawning.

On distribution, it was brought out that pelagic armorhead exhibit an antitropical distribution; therefore, they are not likely to occur in tropical waters. In the Southern Hemisphere, the species of pelagic armorhead that occurs nearest to tropical waters in the Pacific are found near Australia at about lat. 30°S, and in the South Atlantic, the Soviets recorded pelagic armorhead from the southwest coast of Africa near lat. 20°S.

Session 5. Summary

86125

RICHARD N. UCHIDA and SIGEITI HAYASI

In the first paper in this session on stock assessment, Wetherall evaluated the condition of the pelagic armorhead stock using a nonlinear autoregressive model of the stock dynamics. Application of the model was hampered by unavailability of crucial statistics on the catches by Soviet trawlers, statistical difficulties in parameter estimation, and likely model misspecification.

Based only on Japanese catch and effort statistics, Wetherall's preliminary analysis suggested that high variability in recruitment was the chief cause of fluctuations in fishing success. The collapse of the fishery in 1978 could not easily be ascribed to excessive trawling effort. Behavior of the fishery in its early years suggested that stock independent recruitment is the norm for pelagic armorhead except at very low stock levels. Because the spawning stock is now severely depressed, a sharp reduction in fishing mortality is worth considering as a way to accelerate the stock's recovery.

In the second paper, Yamamoto presented an assessment of the stock of alfonsin in the vicinity of the Izu Islands. He noted a drastic change in fishing methods in 1978, from the "drifting barrel operation" to the more efficient "vertical bottom longline" type of fishing. His analysis revealed that the alfonsin stocks inhabiting grounds around Aoga Shima and Tori Shima have declined in recent years, possibly as a result of expansion of fishing.

In the ensuing general discussion, Wetherall pointed out that for the central North Pacific seamount fishery, the decline in catch per unit effort (CPUE) for pelagic armorhead may give an exaggerated picture of the actual armorhead stock decline, if there has been a change in trawling strategy to target alfonsin. The importance of documenting the history of trawling practices and possible changes in fishing strategy and tactics was emphasized.

To a question on the level of the spawning stock of pelagic armorhead, Wetherall replied that the stock is very much depressed, probably by at least an order of magnitude below its condition before the collapse. In related discussions, he added that he has not specifically studied any density-dependent responses of pelagic armorhead, but noted that the average size of armorhead in the catch increased when CPUE dropped drastically, suggesting the possibility of density-dependent growth in the prerecruit stages.

It was suggested during the discussion that the preexploitation stock of pelagic armorhead was probably small because the seamounts provided only limited habitat.

To a question on whether the pelagic armorhead stock assessment model is completely dependent on catch data, Wetherall replied that the model is based on the type of data now available, but is sufficiently flexible to allow modification as more information is acquired. Wetherall pointed out that the model explicitly considered only the adult stage of the pelagic armorhead and does not yet use input on the early life history phases. Conceptually, to model the prerecruit phases information on oceanographic processes and early life conditions might be incorporated, but such elaborations of the armorhead stock model would require very costly and sophisticated research and may never be feasible.

In discussions of the potential of tagging pelagic armorhead for population studies, scientists from the Honolulu Laboratory reported on their experiences in this area and indicated that such tagging is not practical. Armorhead caught on handlines are in poor condition when brought aboard, and when held in baitwells on the research vessel, or tagged and held for observation, they soon die.

It was suggested that future armorhead studies should be directed toward a critical examination of productivity over the seamounts and a study of factors affecting the distribution, development and survival of eggs, larvae, and other early life stages. Additionally, studies should focus on age composition of the seamount armorhead population. It was pointed out that through age determination it would be possible to critically examine aspects of the life history presented in an earlier session. Age and growth studies at the Honolulu Laboratory have just begun, but if the results of preliminary work are validated, life history models of pelagic armorhead could change significantly from those now described in the literature. For example, it may be found that the "fat" pelagic stage of armorhead is indeed recruited to the seamount population at an age of 2 years, as the stock model tentatively assumes. It may also be found that there is a narrow range of ages in the spawning stock, and few older individuals. If so, one might speculate that death soon after spawning is highly probable, if not certain.

In the general discussion regarding alfonsin, it was remarked that the percentage of alfonsin in the ichthyofauna is relatively large in the Emperor Seamount area compared to its representation elsewhere in its range. It was also noted that the catch of alfonsin from the Emperor Seamounts in recent years has been larger than that made in Japanese coastal waters. The relationship between alfonsin stocks in the two areas is unknown. In particular, it is not known to what degree alfonsin yields on the seamounts might be affected by fishing effort and biological production elsewhere.

86126

Session 6. Summary

RICHARD N. UCHIDA and SIGEITI HAYASI

The single paper presented in this session reviewed gaps in our knowledge about seamount populations, discussed the reasons for enhanced productivity over seamounts including Taylor column formation, and looked at potential recruitment mechanisms of demersal populations. Much of the presentation addressed future research directions including resource-associated questions and mechanistic questions.

Resource issues that need to be addressed include research on stock structure, reproduction and behavioral biology, life history, and population assessment. Furthermore, research must be conducted to gain a better understanding of the trophic relationship of pelagic and demersal species.

Mechanistic questions would address such problems as factors important in maintaining large populations on seamounts, sampling strategy to measure physical parameters, and determining primary and secondary productivity and their variability in the vicinity of seamounts.

During the ensuing discussion, a question posed was whether studies should be concentrated on extreme edges of seamount chains or on all of them within the chain. The reply indicated that research should be centered around several seamounts in one area of the chain rather than to confine it to the extremes or to expand the investigation to try to cover everything within the chain. From the standpoint of physical oceanographic research, it was brought out that good results could be obtained from sampling just two or three selected seamounts which would provide comparative data on different kinds of interaction one is likely to see between currents and seamounts.

Discussion brought out that seamount investigation should not be construed as research on an isolated ecosystem. Rather, the investigators should include other seamounts to get an accurate picture of the total ecosystem in the vicinity of seamounts. In describing where pelagic armorhead and alfonsin would fit into the ecosystem, it was suggested that these two species would probably be included in a demersal-benthos ecosystem.

A question of whether pelagic armorhead is epipelagic or mesopelagic stimulated much discussion. Small to large pelagic armorhead can be found at shallow depths of less than 200 m in the pelagic environment. This brought out a question of whether "fat" fish can be actually thought of as pelagic, as advocated by the hypothesized life history and also whether lean fish are pelagic at some point. Sasaki replied that he did not think that "lean" fish were in the pelagic phase.

Attention was then focused on prey items of the pelagic armorhead and alfonsin. Because many prey items were also found associated with the deep scattering layer, it was pointed out that both species can obtain food energy from the pelagic as well as the benthic regime.

It was also brought out that juvenile pelagic armorhead have been found in dense aggregations by whaling ships in the Gulf of Alaska and that stomach contents from whales included this species. It was suggested that in studying the transfer of energy among seamount-associated resources, a more productive approach would be to back calculate the biological production from higher to lower trophic levels than vice versa.

The discussion session was also opened to allow a brief presentation of the results of a study on aspects of seamount ecology in waters off the Southern California Bight and in the mid-Pacific. Genin reported that the physical phenomena induced by the presence of a seamount would primarily affect the benthic and epibenthic communities on these and adjacent seamounts rather than the local epipelagic realm. Intense current sweeping past the seamount summit would prevent sediment accumulation but would enhance the filtering rate of suspension feeders which dominated the benthic community over the seamount.

86127

FOREWORD

RICHARD N. UCHIDA,
SIGEITI HAYASI,
GEORGE W. BOEHLERT

The trawl fishery for pelagic armorhead, *Pseudopentaceros wheeleri* (formerly referred to as *Pentaceros richardsoni*), and alfonsin, *Beryx splendens*, over the central North Pacific seamounts has a relatively short history. Before 1967, fishery scientists were generally unaware of the resources on seamounts; however, the discovery of commercial concentrations of pelagic armorhead on seamounts in the southern Emperor Seamounts by a Russian commercial trawler in November 1967 led to almost immediate exploitation of the species by the Soviets. Unconfirmed reports indicated that the schools of pelagic armorhead on the seamounts averaged 30 m thick and catches averaged from 3 to 50 metric tons on 10-20 min hauls (Sakiura 1972).

Japanese trawlers entered the fishery in 1969. To assist in the development of this fishery, Japanese research vessels conducted extensive surveys in 1972 on the distribution and potential for development of the pelagic armorhead and alfonsin resources. The results of their surveys to the central North Pacific and mid-Pacific seamounts showed that many had summits that were too deep for trawling. Those found suitable were concentrated in the southern Emperor-northern Hawaiian Ridge.

When the U.S. Magnuson Fishery Conservation and Management Act was implemented on March 1, 1977, the U.S. Government assumed exclusive management authority over all fishery resources within 200 mi of its territories except for highly migratory species (tunas). The resources on Hancock Seamounts, which are within the U.S. fishery conservation zone, in some years contributed significantly to the central North Pacific pelagic armorhead catch by the Japanese.

Despite the discovery of the pelagic armorhead resource over the central North Pacific seamounts some 17 years ago, not much is known about the life history, stock structure and identity, and population dynamics of the species. For example, in attempting an assessment of the pelagic armorhead stock, Wetherall (1978) noted a glaring lack of essential data and information on which to base his study.

Because of the inadequacy of information needed to understand the dynamics of the seamount population, the Honolulu Laboratory included seamounts in the massive Northwestern Hawaiian Islands investigation which began in October 1976. Because research on spiny lobster and bottom fish was given higher priority than seamount surveys, however, baseline data on seamount species remained inadequate for a meaningful evaluation and assessment of the stock. In 1982, the Honolulu Laboratory produced a planning document which proposed to upgrade the seamount project into a major seamount-groundfish initiative. This document reiterated the problem of inadequate data and proposed ways to obtain data essential for characterizing standing crop, productivity, trophic interactions, and population dynamics of the resource.

As the initiative developed, the Honolulu Laboratory found that there was a vital need to review the history of the fishery, to assess its present status, and to determine the direction of future research. Since it appeared that the greater part of the exploitation of the seamount groundfish involved Japanese trawling, the Honolulu Laboratory proposed in early 1983 to the Far Seas Fisheries Research Laboratory, Japan Fisheries Agency, in Shimizu, Japan, to convene a joint seamount workshop, which later expanded to include the Japanese Society of Fishery Oceanography of Tokyo, Japan, as a cosponsor. The objectives of the workshop were to review (1) what is known of the oceanography in the vicinity of seamounts, (2) the various fisheries associated with seamounts, and (3) the population characteristics and biology of seamount species (including a preliminary assessment of the stocks), and to develop hypotheses and models to guide the direction of future research.

The workshop was held on March 21-23, 1984 at the Orido Community Center, located near the Far Seas Fisheries Research Laboratory, and at the Government Port Building in Shimizu. This report includes the papers presented as well as summaries of each session prepared by the workshop cochairmen. Appendix lists the participants.

We would like to express our gratitude to two individuals who helped immensely with this volume. Dr. Hajime Yamanaka provided significant editorial work on several Japanese contributions, and Mr. Tamio Otsu translated several contributions from Japanese to English. This version, with all papers in a single language, would have been impossible without their help.

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86128

CORYPHAENIDAE — Dolphin

by James H. Uchiyama

Valid name	*Coryphaena hippurus* Linnaeus 1758 (Fig. 59)
Synonymy	*Scomber pelagicus* Linnaeus 1758 *Coryphaena fasciolata* Pallas 1770 *Coryphaena imperialis* Rafinesque 1810 *Lepimphis hippuroides* Rafinesque 1810 *Coryphaena immaculata* Agassiz in Spix and Agassiz 1829 *Coryphaena marcgravii* Valenciennes in Cuvier and Valenciennes 1833 *Coryphaena suerii* Valenciennes in Cuvier and Valenciennes 1833 *Coryphaena dorado* Valenciennes in Cuvier and Valenciennes 1833 *Coryphaena virgata* Valenciennes in Cuvier and Valenciennes 1833 *Coryphaena argyrurus* Valenciennes in Cuvier and Valenciennes 1833 *Coryphaena vlamingii* Valenciennes in Cuvier and Valenciennes 1833 *Lampugus siculus* Valenciennes in Cuvier and Valenciennes 1833 *Coryphaena scomberioides* Valenciennes in Cuvier and Valenciennes 1833 *Coryphaena nortoniana* Lowe 1839 *Ecterias brunneus* Jordan and Thompson 1914 (from Palko et al. 1982)
Common and vernacular names	Dolphin; mahimahi

Distribution

Circumtropical but also in warm waters between lat. 45°N and 45°S. Captured by surface trolling from Nihoa to Kure Atoll in the NWHI. Larvae and juveniles nektonic, generally pelagic but have been found inshore. Adults inhabit open ocean but also approach coastal waters. They often follow ships and tend to aggregate under floating objects. Small fish (<2.3 kg) are plentiful in summer; large fish (13.6-18.1 kg) are caught mostly from February to April (Squire and Smith 1977).

Distinguishing characteristics

D. 55-65; A. I-III, 25-30; P1. I, 17-21; P2. I, 5; LLs. 245-280. Gill raker counts decrease with age; juveniles have 10-15; whereas adults have 8-10 (Gibbs and Collette 1959). Body elongate, laterally compressed with single dorsal fin originating at nape, extending to caudal; anal fin slightly longer than half of body length; pelvic fins fit into groove in body; caudal fin deeply forked. Species sexually dimorphic. In males, pronounced bony crest on front of head; in females, forehead slightly convex. Terminal mouth extends to vertical axis through middle of eye in both sexes. Males larger than females. Lateral line curved upward above the pectoral.

Color in life variable but usually brilliant green on back, yellow to golden hues on sides, and yellow to white on bottom. Many small brilliant phosphorescent blue and black spots on head and body. Dorsal and anal fins dark.

Life history

The species is heterosexual. In the NWHI, well-developed and ripe ovaries were collected in March-September. Around the main islands, dolphin spawns throughout the year as evidenced by occurrence of juveniles in all months.[15]

Females begin to mature at 35 cm FL; all are mature at 55 cm (Beardsley 1967). Fecundity estimates were from 240,000 to 3,000,000 eggs per fish annually, depending on size.

The buoyant, colorless, spherical eggs measure about 1.2-1.6 mm in diameter and have a single, light-yellow oil globule 0.3-0.4 mm in diameter. The yolk appears to be coarsely segmented. The NMFS culture experiments demonstrated that eggs measure 1.58 mm in diameter and fertilized eggs hatch in 40-53 h at 24-26°C. At hatching, the larvae are 3.95 to 5.10 mm long.[16] The larvae absorb the yolk sac in 2-4 days (Mito 1960; see footnote 16). Male dolphin grow rapidly attaining 20 kg in the first year in Hawaiian waters (Uchiyama et al. 1986).

Dolphin are active and voracious feeders and prefer fast-moving large prey (Welsh 1950). Juveniles feed primarily on copepods; larger juveniles feed on fish and cephalopods (Shcherbachev 1973). Adults feed mainly on fish with flyingfish predominating (Welsh 1950; Ronquillo 1953; Tester and Nakamura 1957; Kojima 1961; Shcherbachev 1973; Rose and Hassler 1974).

Little is known about migration. The dolphin has long been known to be associated with drifting objects (Gooding and Magnuson 1967).

The species tend to school by sex as well as by size (Gibbs and Collette 1959; Kojima 1966; Beardsley 1967).

Dolphin caught during the NWHI investigations ranged from 52.2 to 130.5 cm among females and 48.3 to 110.0 cm for males. The length-weight relationship of dolphin in Hawaii is:

$$W = 6.359 \times 10^{-5} L^{2.7111},$$

where W = weight (lb) and L = fork length (cm) (Tester and Nakamura 1957). Due to sexual dimorphism, this relationship holds only for fish <68 cm. For fish >68 cm, males are heavier than females of the same length.

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[15] Burch, R. K., Biologist, Waikiki Aquarium, Honolulu, HI 96815, pers. commun. May 1982.

[16] Kazama, T. K., Fishery Biologist, Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, pers. commun. 6 April 1984.

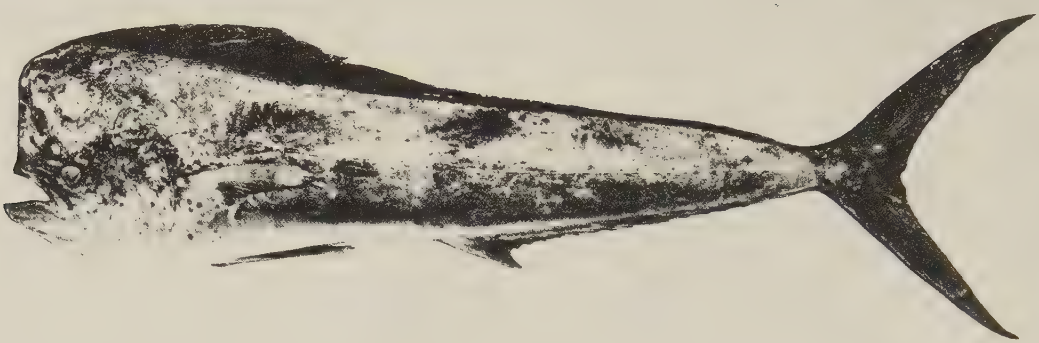

Figure 59.—Male *Coryphaena hippurus*.

Gear and catch

Dolphin is caught mainly by trolling but also taken incidentally by longline and pole and line. For 1961-79, the annual landings varied from 26,526 to 79,492 kg and averaged 50,556 kg.

86129

SCOMBRIDAE — Bigeye Tuna

by James H. Uchiyama

Valid name	*Thunnus obesus* (Lowe 1839) (Fig. 75)
Synonymy	*Thynnus obesus* Lowe 1839 *Thynnus sibi* Temminck and Schlegel 1844 *Orcynus sibi* Kitahara 1897 *Thunnus sibi* Jordan and Snyder 1901 *Germo sibi* Jordan and Snyder 1901 *Thunnus mebachi* Kishinouye 1915 *Parathunnus mebachi* Kishinouye 1923 *Parathunnus sibi* Jordan and Hubbs 1925 *Parathunnus obesus* Jordan and Evermann 1926 *Thunnus obesus* Fraser-Brunner 1950 *Parathunnus obesus mebachi* Jones and Silas 1960 *Thunnus obesus sibi* Jones and Silas 1963 *Thunnus obesus mebachi* Jones and Silas 1964 (from Gibbs and Collette 1967)
Common and vernacular names	Bigeye tuna; poo-nui; mebachi shibi

Distribution

Occurs throughout the Hawaiian Archipelago, however, caught only at Ladd and Nero Seamounts and Raita Bank in NWHI during NMFS surveys. Young bigeye tuna (<20 kg) usually associated with shallow banks. Large individuals believed to inhabit deeper waters between 150 and 200 m (Hanamoto 1976).

Distinguishing characteristics

D. XIV, 15; A. 14 (Godsil and Byers 1944); Gr. 23-31 (Gibbs and Collette 1967). Body fusiform, slightly compressed laterally; dorsal fins separated by a narrow interspace; caudal fin lunate; pectoral fins extend past the anterior edge of second dorsal; two interpelvic processes between pelvic fins; second dorsal and anal fins only slightly higher than first dorsal; 8-10 dorsal, 7-10 anal finlets. Head conical with a terminal mouth which extends back to vertical axis through eye. Head and eye proportionally large. Head length nearly equal to body depth in young, less than equal in older individuals. Body covered with small scales; indistinct corselet. Ventral surface of liver striated. Keel well developed on caudal peduncle and extends to caudal fin where it is surrounded by two small keels (Gibbs and Collette 1967; Fischer and Whitehead 1974).

In life, dark blue to black dorsally, silvery white ventrally. Iridescent greenish-yellow patch present from eye to above base of pectoral; second dorsal and anal fins light yellow; finlets bright yellow with black edges (Gibbs and Collette 1967).

Life history

The species is heterosexual and has no external characteristics to distinguish males from females. In Hawaiian and central Pacific waters, females attain sexual maturity and spawn at 14-20 kg (Yuen 1955). The spawning area of the species is between lat. 12°N-12°S and long. 120°E-110°W (Kikawa 1962). Spawning occurs throughout the year in the equatorial region, but peaks from April through September (Kikawa 1962). Fecundity estimates for a single spawn range from 2.9 to 6.3 million eggs for fish 39 to 107 kg (Yuen 1955).

Newly hatched larvae are 1.5 mm in total length (Kume 1962). Growth is rapid but sexually dimorphic. Males attain a size of 23.7 kg in 2 years, 46.3 kg in 3 years, 66.7 kg in 4 years, and 115.3 kg in 7 years. For females, the sizes attained were 23.9 kg in 2 years, 45.7 kg in 3 years, 64.0 kg in 4 years, and 103.8 kg in 7 years (Shomura and Keala 1963).

Bigeye tuna feeds opportunistically on fishes, squids, other molluscs, and crustaceans. Small individuals (<140 cm FL) consume a larger proportion by volume of crustaceans and fishes and a smaller proportion of molluscs than large individuals (>140 cm) (King and Ikehara 1956).

The length-weight relationship of bigeye tuna is:

$$W = 8.071 \times 10^{-5} L^{2.90182},$$

where W = weight (lb) and L = fork length (cm) (Nakamura and Uchiyama 1966).

Gear and catch

In the Hawaiian fishery, bigeye tuna annual landings in 1961-79 varied widely from 77,064 to 553,744 kg and averaged 280,141 kg. Most of the fish were caught around the main islands by longline vessels; however, since 1971, the ika-shibi fishery using handline has developed significantly and contributed a large proportion to the statewide landings.

In the NWHI the species is caught primarily by Japanese longliners and baitboats, which produced an estimated 1,510 and 734 MT, respectively, from within the FCZ around the Hawaiian Islands in 1977 (Yong and Wetherall 1980).

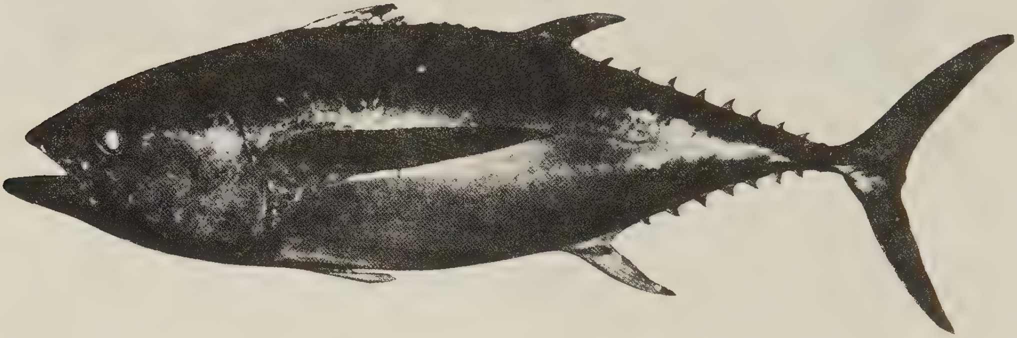

Figure 75.—*Thunnus obesus.*

86130

SCOMBRIDAE — Kawakawa

by James H. Uchiyama

Valid name	*Euthynnus affinis* (Cantor 1850) (Fig. 72)
Synonymy	*Thynnus affinis* Cantor 1850
	Thynnus thunnina Temminck and Schlegel 1850
	Auxis taso Bleeker 1850
	Euthynnus alletera Jordan, Tanaka and Snyder 1913
	Euthynnus yaito Kishinouye 1923
	Gymnosarda alletteratus Meek and Hildebrand 1923
	Wanderer wallisi Whitley 1937
	Euthynnus affinis affinis Fraser-Brunner 1949
	Euthynnus affinis yaito Fraser-Brunner 1949
	Euthynnus alletteratus affinis De Beaufort 1951
	Euthynnus wallisi Whitley 1964
	(from Yoshida 1979)
Common and vernacular name	Little tuna; kawakawa

Distribution

Occurs around the main islands and in the NWHI from Middle Bank to Kure Atoll.

Completes its entire life cycle within the coastal province. Larvae captured in midocean probably carried away from coastal areas by prevailing currents (Yoshida 1979).

Distinguishing characteristics

D. XIV-XV, 12-13; A. 13-14; Gr. 7-9+1+22-24 (Godsil 1954). Body elongated, robust, and fusiform; two dorsal fins separated by a narrow interdorsal space, eight dorsal and seven anal finlets, and a lunate caudal fin. Pectoral fins not extending to interdorsal space. Body naked except for a corselet and lateral line. Snout pointed with a terminal mouth, which extends to or slightly beyond the vertical axis through the middle of the eye. Caudal keels not well developed.

In life, blue to indigo background up to the middle of the first dorsal fin on the back superimposed by black wavy lines. Top of the head and corselet black to dusky and sides of head silvery. Lower half of body silvery white. Black or dusky spots between the pectoral and pelvic fins but not always conspicuous (Godsil 1954; Fischer and Whitehead 1974).

Life history

Kawakawa is heterosexual; males and females are externally similar. There is no record of hermaphroditism. In the NWHI, milt was found in the testes of a male 40.9 cm FL, and ovaries in the developing stage were found in females as small as 38 cm FL. The spawning season is probably during the summer although spent ovaries were found in fishes captured in March and November.

Fecundity estimates of Indian Ocean kawakawa are 0.21 million eggs per spawning and 0.79 million eggs per year for a 48.0-cm fish and 0.68 million eggs per spawning and 2.5 million eggs per year for a 65.0-cm fish (Rao 1964).

Kawakawa has been induced to spawn in captivity (Kaya et al. 1981). Growth is rapid. In the NWHI kawakawa attains a length of 40 cm in 1 year and 67 cm in 2 years (Uchiyama 1980).

Kawakawa feeds opportunistically on crustaceans, fishes, and squid (Welsh 1950; Tester and Nakamura 1957).

Nothing is known about the migratory habits of the species. Because kawakawa are seldom caught beyond 20 nmi from an island or bank, they are thought to be constantly associated with coastal areas or submerged banks.

The length-weight relationship of kawakawa from Hawaiian waters is:

$$W = 2.3829 \times 10^{-5} L^{3.1544},$$

where W = weight (lb) and L = fork length (cm) (Tester and Nakamura 1957).

Gear and catch

The species frequently comprises the incidental catch of the pole-and-line skipjack tuna fishing vessels operating in Hawaiian waters. It is also taken by trolling. Annual landings of kawakawa in 1961-79 ranged from 936 to 43,862 kg and averaged 19,074 kg. The species is of minor importance in the commercial fishery in Hawaii.

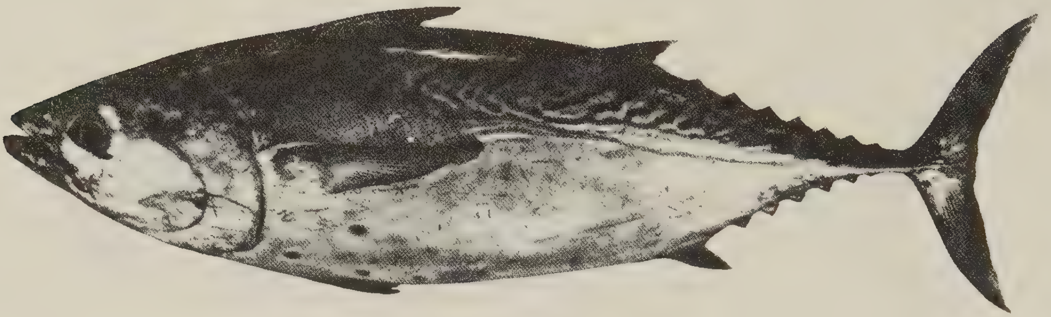

Figure 72.—*Euthynnus affinis*.

86131

SCOMBRIDAE —— Skipjack Tuna

by James H. Uchiyama

Valid name	*Katsuwonus pelamis* (Linnaeus 1758) (Fig. 73)
Synonymy	*Scomber pelamis* Linnaeus 1758 *Scomber pelamys* Bloch and Schneider 1801 *Scomber pelamides* Lacepède 1802 *Thynnus pelamis* Risso 1826 *Thynnus vagans* Lesson 1828 *Thynnus pelamys* Cuvier and Valenciennes 1831 *Pelamys pelamys* Bleeker 1862 *Orcynnus pelamys* Poey 1868 *Euthynnus pelamys* Jordan and Gilbert 1882 *Gymnosarda pelamis* Dresslar and Fesler 1889 *Euthynnus pelamis* Smitt 1893 *Katsuwonus pelamys* Kishinouye 1915 *Gymnosarda pelamys* Thompson 1918 *Katsuwonus pelamis* Kishinouye 1923 *Katsuwonus vagans* Jordan, Evermann, and Clark 1930 *Katsuwonus pelamis* Herre 1933 *Euthynnus* (*Katsuwonus*) *pelamis* Fraser-Brunner 1950 (from Matsumoto et al. 1984)
Common and vernacular names	Skipjack tuna; aku

Distribution

Distributed throughout the Hawaiian Archipelago. Usually occurs in surface schools associated with bird flocks.

Distinguishing characteristics

D. XIV-XV, I, 13-14; A. II, 12-13; P1. 26-27; 7-9 dorsal and 7-8 anal finlets (Waldron 1963). Body elongate, robust, rounded in cross section, fusiform; two dorsal fins separated by a small interspace not larger than eye diameter; tail lunate; anal fin under second dorsal pectoral fins short, triangular; two flaps between pelvic fins. Head conical, mouth terminal, large; maxillary extends to about vertical axis through eye; body naked except for corselet and lateral line. Strong keel present on both sides of caudal peduncle with two smaller keels at caudal end.

In life dark purplish blue dorsally with occasional flashes of irregular line patterns of bright phosphorescent blue. Lower sides and belly silvery with four to six dark longitudinal bands.

Life history

Spawning occurs in late February-September in Hawaiian waters (Brock 1954). Skipjack tuna reaches sexual maturity at about 40-45 cm FL (about 1 year old) (Brock 1954). Fecundity estimates range from 290,000 to 1,880,000 eggs per spawning for fish 43.8 to 86.7 cm long (Morris 1966). Skipjack tuna are believed to be multiple spawners (Brock 1954; Morris 1966).

Fertilization is external (Waldron 1963). Fertilized eggs hatch in 30-31 h at 25°-26°C (Kaya et al. 1982). The larvae average 2.94 mm at hatching.[26] Growth is rapid; the fish reaches 44 cm in 1 year, 68 cm in 2 years, and 82 cm in 3 years (Uchiyama and Struhsaker 1981). The species attains 90 cm in Hawaiian waters.

Skipjack tuna feeds on a wide variety of organisms. Stomach contents of central Pacific fish consist primarily of fish; molluscs rank second, and crustaceans third (Yuen 1959; Waldron and King 1963). During summer, large skipjack tuna (>60 cm) feeds primarily on fish (90%); whereas among smaller fish (<60 cm) crustaceans and molluscs are predominant (Yuen 1959).

Skipjack tuna is known to migrate long distances. Fish tagged in the eastern and western Pacific have been recovered in Hawaiian waters (Josse et al. 1979).

Short-term local movement of skipjack tuna has been studied using sonic tags. A school of small skipjack tuna spent the day on the bank and off the bank at night (Yuen 1970). Small skipjack tuna also appears to keep its association with a school for a long time and remains in the same area for almost 3 months (Yamashita and Waldron 1959). Large skipjack tuna (ca. 70 cm) apparently behaves differently (Dizon et al. 1978). It is independent of bank and remains in waters above 20°C 85% of the time, occasionally making excursions into cold water.

The length-weight relationship of central Pacific skipjack is:

$$W = 4.546 \times 10^{-9} L^{3.36836},$$

where W = weight (lb) and L = fork length (mm) (Nakamura and Uchiyama 1966).

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[26] Hendrix, S. B. 1982. Factors affecting the growth and survival of skipjack tuna, *Katsuwonus pelamis*, larvae reared in the laboratory. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, Admin. Rep. H-82-23C, 15 p.

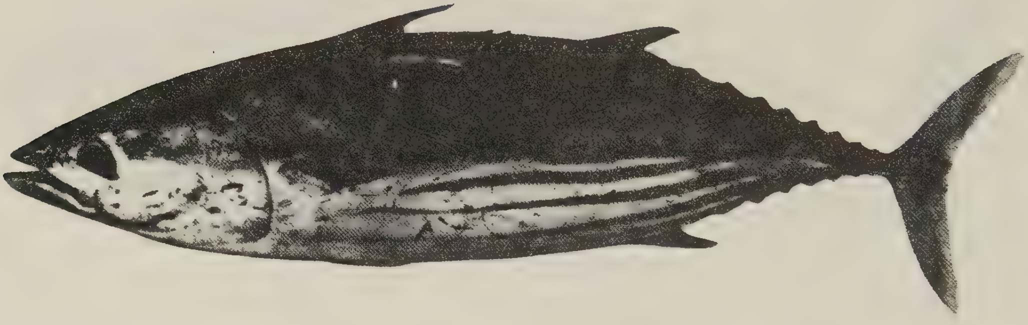

Figure 73.—*Katsuwonus pelamis*.

Gear and catch

In Hawaiian waters, the species is caught almost exclusively by pole and line and live bait; small quantities are also landed by trolling. Descriptions of the fishery and trends in catches are found in June (1951) and Uchida (1966, 1967, 1976).

Annual landings of skipjack tuna in 1961-79 from water around the main islands fluctuated widely from 2,292 to 7,329 MT and averaged 4,073 MT. Currently, there is no Hawaiian fishery for the species in the NWHI. A pole-and-line, live bait fishery, however, was known to operate in the NWHI during the 1970's as an outgrowth of the Japanese albacore fishery. In the summer of 1977, the Japanese harvested an estimated 4,375 MT within the FCZ of the NWHI (Yong and Wetherall 1980).

by James H. Uchiyama

Valid name *Thunnus albacares* (Bonnaterre 1788) (Fig. 74)

Synonymy
Scomber albacares Bonnaterre 1788
Scomber albacorus Lacepède 1800
Thynnus argentivittatus Cuvier and Valenciennes 1831
Scomber Sloanei Cuvier and Valenciennes 1831
Thynnus albacora Lowe 1839
Thynnus macropterus Temminck and Schlegel 1844
Thunnus argentivittatus South 1845
Orcynus subulatus Poey 1875
Orcynus albacora Poey 1875
Orcynus macropterus Kitahara 1897
Germo macropterus Jordan and Snyder 1901
Thunnus macropterus Jordan, Tanaka, and Snyder 1913
Thunnus allisoni Mowbray 1920
Germo argentivittatus Nichols and Murphy 1922
Germo allisoni Nichols 1923
Neothunnus macropterus Kishinouye 1923
Thunnus subulatus Jordan and Evermann 1926
Neothunnus catalinae Jordan and Evermann 1926
Neothunnus albacora Jordan and Evermann 1926
Neothunnus itosibi Jordan and Evermann 1926
Neothunnus albacores Jordan and Evermann 1926
Neothunnus allisoni Jordan and Evermann 1926
Kishinoella zacalles Jordan and Evermann 1926
Semathunnus guildi Fowler 1933
Semathunnus itosibi Fowler 1933
Neothunnus argentivittatus Beebe and Tee-Van 1936
Germo albacora Fowler 1936
Thunnus albacora Tortonese 1939
Germo itosibi Smith 1949
Neothunnus albacora brevipinna Bellón and Bardán de Bellón 1949
Neothunnus albacora longipinna Bellón and Bardán de Bellón 1949
Neothunnus macropterus macropterus Bellón and Bardán de Bellón 1949
Neothunnus macropterus itosibi Bellón and Bardán de Bellón 1949
Neothunnus brevipinna Postel 1950
Thunnus zacalles Fraser-Brunner 1950
Thunnus albacares Ginsburg 1953
Thunnus catalinae Ginsburg 1953
Neothunnus albacores Mather 1954
Thunnus albacares Le Danois 1954
Neothunnus albacora macropterus Schultz 1960
Thunnus albacares macropterus Jones and Silas 1963
Thunnus itosibi Jones and Silas 1963
(from Gibbs and Collette 1967)

Common and vernacular names Yellowfin tuna; ahi

Distribution

Occurs throughout the Hawaiian Archipelago.

Distinguishing characteristics

D. XIV-II, 12; A. II, 12 (Jordan and Evermann 1905). Body fusiform, slightly compressed laterally. Two dorsal fins separated by a narrow interspace; caudal fin lunate; moderately long pectoral fins reach beyond origin of second dorsal but not beyond end of its base; a pair of interpelvic processes between pelvic fins. On some large specimens the second dorsal and anal fins long (20% of FL). Head conical, terminal mouth reaching vertical axis through anterior of eye. Body wholly covered with small scales; corselet present. Well-developed keel on each side of the caudal peduncle between two small keels at the caudal end; 8-10 dorsal and 7-10 anal finlets

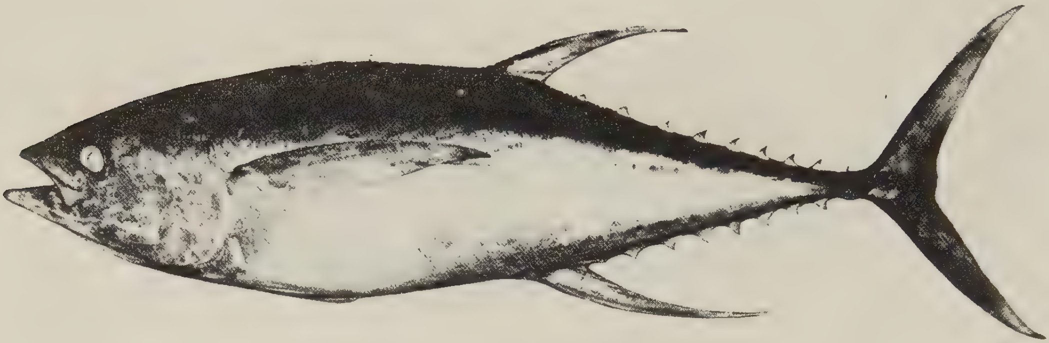

Figure 74.—*Thunnus albacares.*

on caudal peduncle. Individuals with undeveloped second dorsal and anal fins resemble bigeye tuna from which it can be distinguished by the lack of striations on the ventral surface of the liver (Fischer and Whitehead 1974).

In life, dark blue to black dorsally, silver ventrally; yellow or golden band occasionally visible from snout to tail on sides. Faint vertical lines alternating with vertical rows of spots present on the ventral half of the body. Dorsal and anal fins, all finlets, and caudal fin bright yellow. Finlets have narrow black border (Gibbs and Collette 1967).

Life history

The species is heterosexual and exhibits no externally visible sexual dimorphism (Cole 1980). Observations during NWHI survey cruises showed that sexually mature males can be as small as 88 cm; whereas the smallest female with ripe ovaries was 116 cm. These sizes at maturity agree with past estimates of sexual maturity for central and western Pacific yellowfin tuna (June 1953; Yuen and June 1957; Kikawa 1962). Spawning occurs from May through October in Hawaiian waters (June 1953). Fecundity estimates range from 2.37 to 8.59 million eggs per spawning for fish 47 to 88 kg (June 1953). The species is a multiple spawner; however, the frequency of spawning per season is undetermined.

Artificially fertilized eggs were observed to hatch in 25-36 h at a water temperature of 23.7° to 27.0°C. The larvae are 2.2 mm at hatching and grow to 3.1 mm in 4 days (Inoue et al. 1974). Growth is rapid; the species attains 53 cm at 1 year and 90 cm at 2 years (Uchiyama and Struhsaker 1981).

Yellowfin tuna around Hawaii feeds on fishes, crustaceans, and molluscs, primarily cephalopods (Welsh 1950; Tester and Nakamura 1957). Small yellowfin tuna (<100 cm) feeds primarily on crustacean larvae; medium-sized fish (100-129 cm) feeds mostly on crustacean larvae and squids; whereas large fish (>130 cm) feeds primarily on fish and squid (Reintjes and King 1953).

Not much is known about the migration of yellowfin tuna in the NWHI. Of 203 fish tagged, there was only a single recovery. The fish moved 31 nmi in 37 days.

The length-weight relationship derived from a sample of 4,822 fish is:

$$W = 3.256 \times 10^{-5} L^{3.05834},$$

where W = weight (lb) and L = fork length (mm) (Nakamura and Uchiyama 1966).

Gear and catch

Yellowfin tuna is caught mainly by longline, pole and line, trolling, and handline (ika-shibi and palu-ahi). Annual landings of this species, second only to skipjack tuna in importance in the Hawaiian fishery, fluctuated widely in 1961-79 from 17,457 to 962,641 kg and averaged 434,624 kg. Most of the fish are taken around the main islands and substantial numbers are now taken off the Island of Hawaii in the ika-shibi fishery (Yuen 1979).

In 1977 in the NWHI, 337 and 403 MT of yellowfin tuna were taken by Japanese baitboats and longliners, respectively (Yong and Wetherall 1980).

86133

GROWTH OF DOLPHINS, *CORYPHAENA HIPPURUS* AND *C. EQUISELIS*, IN HAWAIIAN WATERS AS DETERMINED BY DAILY INCREMENTS ON OTOLITHS

The dolphin, *Coryphaena hippurus*, and pompano dolphin, *C. equiselis*, are widely distributed pelagic fishes in tropical and subtropical oceans (Beardsley 1967; Rose and Hassler 1968; Shcherbachev 1973). In Hawaiian waters *C. hippurus* is caught throughout the year, but its abundance fluctuates. Small fish (<2.3 kg) are plentiful in summer and large fish (13.6-18.1 kg) are more abundant from February to April (Squire and Smith 1977). *Coryphaena hippurus* is important to the commercial and recreational fisheries; *C. equiselis*, a smaller fish with a maximum length of 74 cm (Herald 1961), is occasionally caught by recreational fishermen. Although much is known about the life history of *C. hippurus* in the Atlantic (Palko et al. 1982), the biology of the Hawaiian population has been only sketchily investigated. Little is known about *C. equiselis*.

At least three age and growth studies on *C. hippurus* have been reported. Annual marks on scales have been used to age *C. hippurus* off Florida (Beardsley 1967) and North Carolina (Rose and Hassler 1968) in the western North Atlantic Ocean. Wang (1979) used monthly modal progression of length-frequency distributions to estimate the growth rate of *C. hippurus* off eastern Taiwan in the western Pacific Ocean. The estimated growth rates of *C. hippurus* off Florida and North Carolina differed slightly, but the growth rate of *C. hippurus* in the western Pacific Ocean was reported to be about twice as great as those in the western North Atlantic Ocean.

The purpose of this study was to validate estimates of age and growth of larval and juvenile *C. hippurus* and *C. equiselis* based on microstructure of otoliths (sagittae) from fish of known age reared in captivity. Otoliths from wild specimens captured in Hawaiian waters were also used as a source of age and growth information and these data were fitted to the von Bertalanffy growth model. Ages of cultured and captured wild specimens were estimated by enumerating presumed daily increments on the sagitta following Pannella (1971). The daily nature of the increments was validated by counts from sagittae of fish reared in captivity and whose age was known. Knowledge of growth rates of both species of dolphins are useful to mariculturists who would like to compare the growth rates of wild and cultured individuals. Information on the growth rate of *C. hippurus* can also be of use to managers of Hawaiian fishery resources.

Materials and Methods

Validation

Fertilized eggs of *C. hippurus* and *C. equiselis* were obtained between January 1982 and February 1983 from captive broodstock held at the University of Hawaii's Waikiki Aquarium (WA); the Kewalo Research Facility (KRF) of the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service; and The Oceanic Institute, Waimanalo, HI. Larvae of both species were reared at the WA in 4,000 L circular fiber glass tanks with flow-through water exchange and under shaded natural light condition. Water temperature ranged between 23° and 27°C. Both species were fed an unlimited supply (a density of 1-5/mL) of cultured copepod, *Euterpina acutifrons*, and *Artemia* sp. until they were large enough to accept chopped fish and squid (about 30 d after hatching), which were then provided several times during the day. These fish were fed to satiation. One 167-d-old and three 191-d-old *C. hippurus* were reared at the KRF under similar environmental conditions and feeding regime as at the WA.[1] These juvenile *C. hippurus* were transferred to 8 m diameter tanks when they were about 25 cm long.

One to three larvae of *C. equiselis* were sampled on the day of hatching (D-0), and each day thereafter (D-1, D-2, D-4, etc.). However, after the fourth day, there were few survivors, so only a single specimen was taken at intervals of 4 d from D-19. Three larvae of *C. hippurus* were sampled on D-4 and single specimens were sampled at various intervals or obtained after accidental deaths for validating the growth increments. Other larvae were sampled from other batches on D-0, D-1, and D-2 for measurements. Specimens were sampled around noon. Total length of the larvae was measured under a microscope with an ocular micrometer while the specimen was alive or within an hour after death. To facilitate measurement, each larva was put on a glass slide, extended to its full length, and measured. For the examination of otoliths, the larva on the slide was immersed in 70% ethanol and allowed to fix for an hour. The larva was then removed from the ethanol bath, blotted, and mounted in Euparal,[2] a water soluble mounting medium, and covered with a cover slip. Otoliths could be examined in the squashed whole mount without extracting them.

After measuring the fork length of juvenile and adult dolphins with a caliper to the nearest millimeter, otoliths were extracted, cleaned, and mounted whole. To extract the otoliths, the head was removed from the body, and the flesh removed from the head to expose the skull. With a saw or knife, most of the supraoccipital and roof of the skull were removed. After careful removal of the brain, the sagittae (largest of the three otoliths) could be found in the sacculi located anteriorly on the right and left sides of the first vertebra at the caudal end of the brain cavity. Under a dissecting microscope, the sagitta was teased out of the sacculus, and extraneous tissues were brushed away. The pair of sagittae was then placed on a clean glass slide, permitted to dry, and mounted in Euparal. Segments of monofilament line slightly thicker than the sagittae were placed on both sides of the sagittae to prevent the cover slip from crushing it.

After clearing for a month, presumed daily increments on a sagitta were enumerated using a compound binocular microscope with transmitted light at 600× magnification. Increments were counted starting from the core out to the edge of the postrostrum, or from the core to the tip of the rostrum. Usually, counts could not be made in a direct line from the core to the edge of the rostrum or postrostrum of the sagitta; rather, a somewhat circuitous route was taken from one area of the sagitta to another by following a prominent growth increment. Increments were also counted inward from the edge to the core. Two independent age estimations were made separately on the rostrum and postrostrum on a sagitta to verify the age of fish. In some samples, it was possible only to make a single age estimate since the sagitta was incomplete, having just a rostrum or postrostrum. The reader had no information such as specimen size or previous counts to prevent bias in the counting.

The arithmetic mean of 3-14 counts was used to estimate a fish's age. The number of counts from the rostrum and postrostrum varied from as few as 3 for a larva to 14 for a sagitta of a juvenile. The relationship between counts of otolith increments and days was assessed for both species by regression analysis.

Growth of Wild Specimens

Juveniles of both species were dip netted from Kaneohe Bay, HI. Large juveniles and adults of both species were obtained from private and chartered sport fishing boats in Honolulu, and *C. hippurus* specimens were also obtained from cruises of the NOAA ship *Townsend Cromwell* to the Northwestern Hawaiian Islands from October 1976 to September 1981. Fork lengths were measured to the nearest millimeter with calipers. The extraction and slide preparation of sagittae, and counting method were the same as described for the validation experiments above. But before reading the sagittae of fish caught in the wild, the sagitta of a known-age fish was reexamined to review the difference between known daily increments and subdaily increments. Concentric daily increments, which consist of an inner light band and an outer dark band, were distinguished from subdaily increments by carefully focusing to the plane of maximum clarity. The dark band of the subdaily increment appeared less defined than the dark band of daily increments. Misinterpretation and counting subdaily increments as daily increments could result in an overestimation of age. The mean of 10-20 counts was used as the age estimate of older fish.

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[1] Thomas K. Kazama, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. commun. October 1984.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Age estimates of wild fish were fitted to the von Bertalanffy growth model using NLIN Procedure, a nonlinear regression routine (SAS Institute 1982). The three juvenile *C. hippurus* whose sex was undetermined were added to both the male and female groups when fitting the curves.

Results

Validation

Fertilized eggs of *C. equiselis* and *C. hippurus* began to hatch after 48-50 h at 24°-25°C and all hatched within 2 h. The larvae of both species were 4.0-4.6 mm TL and had two pairs of otoliths, the sagitta and lapillus, at time of hatching. Otoliths of *C. equiselis* and *C. hippurus* on D-0 ranged from 16 to 20 μm in diameter and consisted of the core and primordium. An hour after hatching, the larvae were from 5.2 to 5.4 mm TL but did not grow during the next 3 d and even shrank from 0.1 to 0.2 mm. Otoliths of both species on D-1 had a dark ring near the edge which the otoliths of D-0 larvae did not have and were 22-24 μm in diameter. The sagittae of both species on D-4 had four increments (Fig. 1) and were now slightly larger than the lapillus. Sagittal diameters were 29-36 μm for *C. equiselis* and 34-41 μm for *C. hippurus.*

Mean counts of growth increments on the sagittae of 10 *C. hippurus* (Table 1) and 13 *C. equiselis*

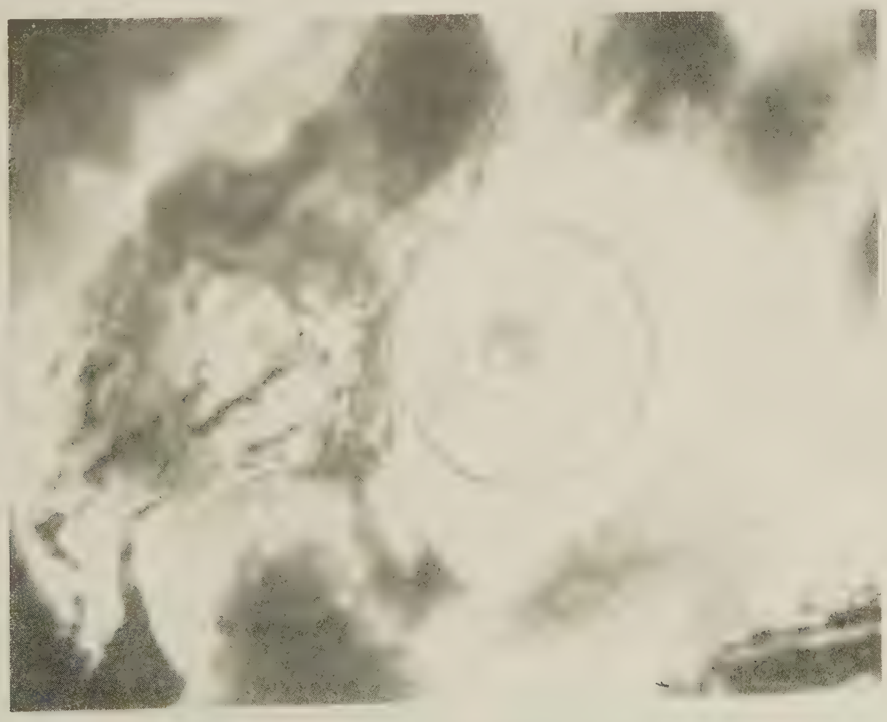

FIGURE 1.—Sagitta of a day-4 *Coryphaena hippurus* larva. Diameter of sagitta is 17 μm.

TABLE 1.—Mean of counts on known age sagittae of *Coryphaena hippurus*.

Known age	Mean increment counts	SD	No. of counts	Total length (mm)	Fork length (mm)
0	0			5.3	
1	1			—	
4	4	0.00	3	6.7	
4	4	0.00	3	6.8	
4	4	0.00	3	6.8	
20	20.0	±1.26	5	—	
35	33.6	±2.06	9	—	—
47	45.2	±3.16	10	—	95.0
167	166.8	±7.14	11	—	383.0
191	190.3	±6.92	6	—	510.0
191	191.0	±0.71	4	—	554.0
191	192.8	±7.44	5	—	491.0

TABLE 2.—Mean counts on known age sagittae of *Coryphaena equiselis*.

Known age	Mean increment counts	SD	No. of counts	Total length (mm)	Fork length (mm)
0	0			4.0	
1	1	0.00	3	—	
1	1	0.00	3	—	
4	3	0.00	3	4.6	
4	4	0.00	3	5.2	
19	19	0.00	3	14.2	
23	23.6	±2.23	8	23.0	
27	21.5	±1.59	14	25.2	
31	31.7	±1.38	7	—	29.5
36	35.3	±2.45	10	—	48.0
51	51.7	±2.13	13	—	82.0
52	53.6	±4.81	14	—	72.0
63	63.3	±3.19	14	—	89.0
63	63.4	±8.59	13	—	112.0

(Table 2) were plotted against corresponding known ages (Figs. 2, 3). The relationships of mean increment counts (Y) to known age (X) were $Y = -0.5295 + 1.0035X$ ($r = 0.999$, $P < 0.01$) for 10 *C. hippurus* and $Y = -0.6986 + 1.0164X$ ($r = 0.997$, $P < 0.01$) for 13 *C. equiselis*. These results demonstrated that growth increments are formed daily, and validated their use for aging wild fish up to 191 d for *C. hippurus* and 63 d for *C. equiselis*.

Growth of Wild Specimens

Because of sexual dimorphism, separate von Bertalanffy growth parameters were calculated for male and female *C. hippurus* (Table 3). The male and female von Bertalanffy growth curves and 18 age-length relationships of *C. hippurus* are shown in

TABLE 3.—Von Bertalanffy growth parameters calculated from captured wild specimens of *Coryphaena hippurus*.

Sex	Number	Parameter	Estimate	SE
Male	10	t_0	0.0790 yr	0.0305
		K	1.1871	0.5218
		L_∞	189.9301 cm FL	48.9702
Female	9	t_0	0.0731 yr	0.0126
		K	1.4110	0.2454
		L_∞	153.2676 cm FL	14.2168

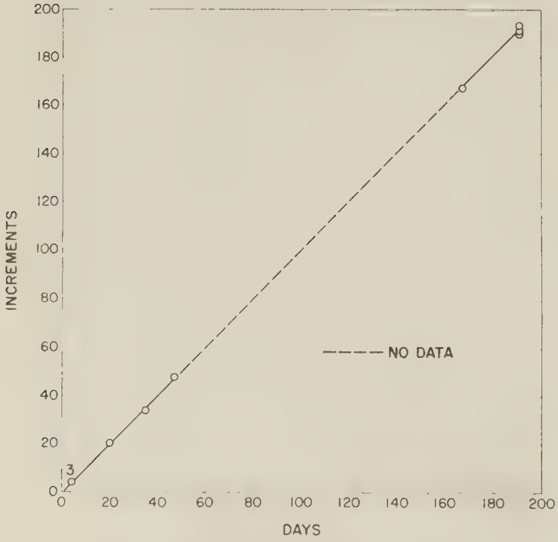

FIGURE 2.—Validation of daily increments on sagittae of *Coryphaena hippurus* by relationship of known age (X) to mean increment count (Y) up to 191 d ($r = 0.999$).

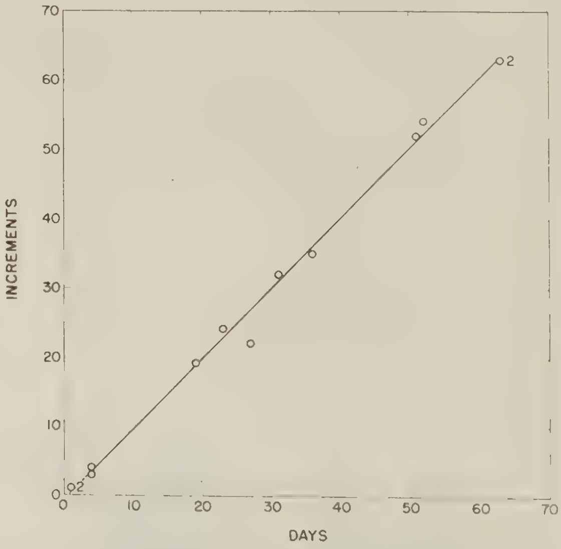

FIGURE 3.—Validation of daily increments on sagittae of *Coryphaena equiselis* by relationship of known age (X) to mean increment count (Y) up to 63 d ($r = 0.997$).

Figure 4. A single set of growth parameters (Table 4) was calculated for *C. equiselis* since the largest specimen in the sample had just reached sexual maturity, and the calculation of separate growth curves by sex was not warranted. The von Bertalanffy growth curve and 13 age-length relationships of *C. equiselis* are shown in Figure 5.

Discussion

Validation

A pair of otoliths was present at the time of hatching for both dolphins, and the first increment was formed on the otoliths on D-1, identical to *Katsuwonus pelamis*, another tropical pelagic species (Radtke 1983). The strong correlation of mean increment counts of sagittae to known age of fish validated the use of growth increments in the aging of *C. equiselis* up to 63 d and *C. hippurus* up to 191 d. Since regular incremental formation began on D-1, no adjustment is required to the incremental counts of wild fish sagittae to estimate age. Ideally, validation of daily increments should cover 1) the time when the first daily increment is formed, 2) the regularity in the formation of increments in all stages of life, and 3) events such as spawning, migration, and periods of starvation which may affect the regularity of increment formation. Having achieved only part of these requirements, validation of daily increments on otoliths should continue as older known-age specimens become available, and the effects of spawning and starvation on increment formation should also be examined.

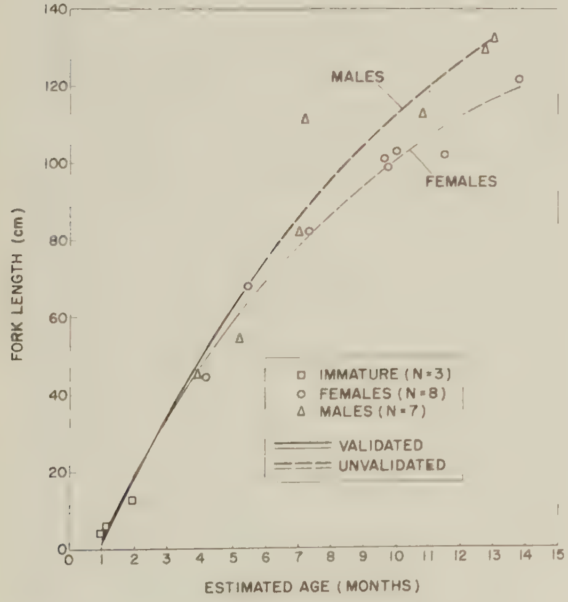

FIGURE 4.—Von Bertalanffy growth curves of male and female *Coryphaena hippurus* in Hawaiian waters.

TABLE 4.—Von Bertalanffy growth parameters calculated from captured wild specimens of *Coryphaena equiselis*.

Number	Parameter	Estimate	SE
13	t_0	0.0648 yr	0.0131
	K	2.1734	0.9750
	L_∞	61.3914 cm FL	17.8000

Growth of Wild Specimens

The plot of age-length relationships of male *C. hippurus* showed that there was at least one extreme variant. This 111.0 cm FL male greatly affected the growth curve, resulting in a lower estimated L_∞ and causing most of the male age estimates to fall below the growth curve (Fig. 4). Thus, age-length relations of wild *C. hippurus* should be examined further to shed light on the extent of variation in size at given ages. Additional age determinations might also improve the confidence intervals of the von Bertalanffy growth parameters.

Growth rates of *C. hippurus* to age 1 around Hawaii appeared to be greater than those reported from the western North Atlantic Ocean. Beardsley (1967) reported a mean length of 72.5 cm in age group 1 for *C. hippurus* off Florida. Rose and Hassler (1968) reported a mean length of 65.3 cm at the end of 1 yr for fish off North Carolina. Around Hawaii male *C. hippurus* were estimated to attain

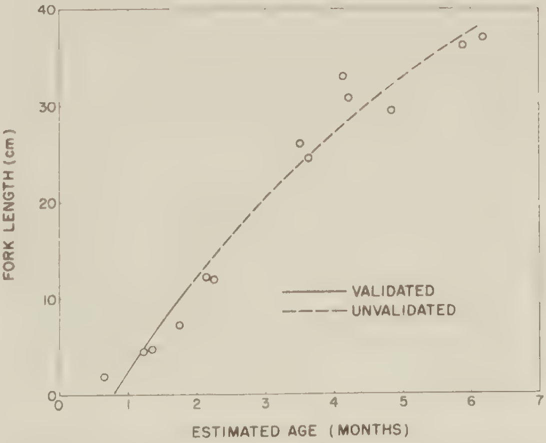

FIGURE 5.—Von Bertalanffy growth curve of *Coryphaena equiselis* in Hawaiian waters derived from 13 age estimates.

a length of about 126 cm at 1 yr and about 112 cm for females. The slower growth rate of *C. hippurus* in the western North Atlantic Ocean may be the result of a decrease in feeding rate when water temperature goes below 23.0°C and a cessation of feeding at 18.0°C (Hassler and Hogarth 1977). *Coryphaena hippurus* feed throughout the year in Hawaii and can be expected to grow continuously.

Wang (1979) used the monthly progression of modes in length-frequency distributions to estimate growth rates of about 10 cm/mo from February through June for *C. hippurus* between 50 and 100 cm FL. This growth rate is similar to that found for *C. hippurus* in Hawaiian waters.

Growth rates of captive *C. hippurus* were similar to those of wild fish in Hawaiian waters. Beardsley (1967) reported rapid growth rates of three captive *C. hippurus*. These fish grew from about 35 to 125 cm in 7 to 8 mo.[3] Soichi (1978) reported that 11 *C. hippurus* 35-50 cm TL grew to a mean 123 cm TL in 7-8 mo. Their observations also support our estimates of rapid growth for *C. hippurus* around Hawaii.

Coryphaena equiselis appeared to grow as rapidly as *C. hippurus* during the first 4 mo, then grew at a slower rate (Fig. 5). At about 4 mo, *C. equiselis* reached sexual maturity. *Coryphaena hippurus* also reached sexual maturity at 4-5 mo, but have been observed to mature as early as 3 mo in captivity.

The daily regularity of increment formation has been demonstrated from D-1 to D-191 for *C. hippurus* and from D-1 to D-63 for *C. equiselis*. So the use of daily increment counts on the sagitta of wild fish for estimating age has only been partially validated for these dolphins. The age-length relationships are valid for the first 6 mo for wild *C. hippurus* and the first 2 mo for wild *C. equiselis*. Thus, the von Bertalanffy growth curves calculated for wild *C. hippurus* in Hawaiian waters should be viewed with caution despite good agreement with several other growth observations in the literature.

Acknowledgments

Our thanks to Richard W. Brill, Richard E. Brock, Leighton R. Taylor, and Jerry A. Wetherall for their critical reviews of this manuscript. Carol Hopper greatly assisted our sampling efforts for wild-caught specimens and Thomas K. Kazama provided the oldest known-age *C. hippurus*.

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JAMES H. UCHIYAMA

Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
P.O. Box, 3830, Honolulu, HI 96812

RAYMOND K. BURCH
SYD A. KRAUL, JR.

Waikiki Aquarium, University of Hawaii
2777 Kalakaua Avenue
Honolulu, HI 96815

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[3] A length-weight relationship (Gibbs and Collette 1959) was used to estimate lengths in centimeters from weights, given in pounds, by Beardsley (1967).

86134

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Fillet Yields of Dover Sole versus Depth of Capture and Length

Edward Ueber

Tiburon Laboratory, Southwest Fisheries Center, National Marine Fisheries Service
3150 Paradise Drive, Tiburon, California 94920, USA

Abstract.—The fillet yield (100% × fillet weight ÷ round weight) of Dover sole (*Microstomus pacificus*) caught off central and northern California was examined with respect to fish total length and depth of capture. The yield from Dover sole caught at depths greater than 458 m was not related to fish length. However, the yield from fish caught at shallower depths was correlated with fish length; the maximum yield was obtained from fish 40–42 cm long. Fillet yield was substantially lower for fish larger than 42 cm. A comparison of the yields of shallow- and deep-caught fish showed that shallow-caught fish had a 4.1% higher yield.

Management of the groundfish resources of California, Oregon, and Washington has received increased attention since enactment of the Magnuson Fishery Conservation and Management Act of 1976. The Pacific Fishery Management Council (PFMC), created under the act, has since initiated a number of studies with the goal of producing equitable and optimal long-term management of the west coast groundfish fishery. My study was undertaken in 1977 to assist the PFMC to determine factors relevant to the long-run output of fish products from west coast groundfish stocks because few yield data were available for the fresh product.

One of the goals of management is to increase productivity. The groundfish plan development team of the PFMC equated long-term productivity of Dover sole (*Microstomus pacificus*), one of the most important groundfish, to the stock's estimated maximum sustainable yield (MSY). To achieve and maintain MSY, management measures may need to be instituted when Dover sole populations show signs of stress (Anonymous 1980). These management measures may include time or area closures, quotas, or gear limitations. Most Dover sole are caught in trawl nets, so it is likely that gear limitations would take the form of an increase in the minimum size of mesh allowed. Larger meshes presumably would allow more small fish to escape and be caught later when they are larger. Also, processors generally prefer larger fish, which they believe yield proportionately more flesh and hence are cheaper to process for that reason. Indeed, Gates and Norton (1974) found this to be true for the yellowtail flounder (*Limanda ferruginea*) fishery in New England.

The chief objective of this study was to determine if the fillet yield of Dover sole, as produced by professional filleters in commercial processing plants, was correlated with fish length. A second objective was to determine if Dover sole from deep water (defined here as deeper than 458 m) gave a lower fillet yield than those caught in shallower water. The fishery for Dover sole is conducted from shallow water out to depths of 1,280 m, and industry members think that those from shallow water yield about 5% more flesh.

Methods

I examined Dover sole landed at northern and central California ports from April 1977 to March 1978. Vessel captains were interviewed to learn whether or not their catches were made in shallow or deep water. At the processing plant, total lengths of fish were measured to the nearest centimeter and grouped into 2-cm size classes separated by 1-cm intervals. This was accomplished by excluding fish that fell within these 1-cm intervals. Each size class of fish was placed in a separate container that was designated as a sample. Only fish 34–54 cm long were measured because smaller fish normally are not filleted and larger fish are rarely caught. Sample weights varied because container size differed at the three processing plants where the study was conducted. Also, partly filled containers were used when no more fish were available. Mean sample weight was 16.8 kg (range, 5.0–27.1 kg) for shallow-water Dover sole and 14.9 kg (range, 3.0–21.2 kg) for Dover sole taken from deep water (Table 1). After the containers were weighed, they were passed to experienced filleters in the plants. The fish were distributed to as many different experienced filleters as possible to reduce bias. When the finished fillets were retrieved, they were weighed and counted to assure that their

TABLE 1.—Number of fish in a sample (N), total sample weights (W, kg), and number of samples (n) related to the total length of Dover sole caught at depths above and below 458 m.

		Depth, sampling date (season)[a]							
		Depth < 458 m, 1977–1978						Depth > 458 m, 1977	
Total-length group (cm)	Variable	Apr 25 (1)	May 2 (1)	Jun 21 (1)	Sep 11 (2)	Dec 20 (3)	Mar 20 (4)	Sep 13 (2)	Dec 21 (3)
34–36	N	104	103	185	340	79	55	98	252
	W	46	43	75	138	34	22	46	110
	n	2	2	2	10	3	2	3	7
37–39	N	0	256	131	231	103	97	294	232
	W		144	60	121	55	51	158	133
	n	0	6	3	8	4	4	11	8
40–42	N	0	292	0	174	79	108	269	151
	W		207		116	55	74	194	106
	n	0	9	0	8	4	5	13	7
43–45	N	57	259	0	278	40	49	150	76
	W	48	220		233	34	44	142	66
	n	2	9	0	16	2	3	9	5
46–48	N	0	95	74	94	24	78	58	29
	W		96	66	96	25	89	62	31
	n	0	4	3	8	2	6	4	2
49–51	N	0	22	35	34	6	40	32	12
	W		28	41	42	8	56	44	15
	n	0	2	3	3	1	4	3	1
52–54	N	4	7	24	3	3	17	10	2
	W	6	9	34	5	5	27	16	3
	n	1	1	2	1	1	2	1	1

[a] Seasons: 1 = April–June; 2 = July–September; 3 = October–December; 4 = January–March.

number was equal to twice the number of fish in the sample.

Results

The fillet yield (100% × weight of fillets ÷ total weight) was calculated for each sample. Although seasonal food availability, sexual mix, and reproductive cycles could have an effect on fillet yield, the shape of the yield curve remained constant. Seasonality could not be separated from location of capture and place of filleting, nor were sexes determined. Therefore, seasonal differences were not statistically compared and all data were combined for each of the two depth strata. The shallow-depth strata combined the data from the four seasons (1 = April–June; 2 = July–September; 3 = October–December; and 4 = January–March) and the deep-depth strata combined seasons 2 and 3. Analysis of variance (Table 2) indicated no significant relationship between fish length and yield for deep-caught fish. However, the yield from shallow-water fish was linked to fish length.

The greatest fillet yield was obtained from fish 40–42 cm in total length (Figure 1). The yield was 1.1% lower for fish 34–36 cm long and 3.7% lower for fish 52–54 cm long. Actual yields are not given because processors who allowed this study to be made in their plants asked that these figures remain proprietary and confidential.

Comparison of season 2 (July–September) fillet yields showed that fish caught in shallow water yielded more fillet flesh than did fish from deep water (Table 2). The relationship between fillet yield and length was not significant. The mean fillet yield was 4.1% greater for shallow-water than for deep-water fish. I do not know why this occurred, but processors believe that flesh of deep-dwelling fish has a higher water content. The reason fish larger than 43 cm had lower fillet yields also is unknown. Perhaps age also affects water content of the flesh, or else gonad development and stomach contents contribute proportionately more to the total weight of larger fish.

Management Implications

The fillet yield of Dover sole appears to be related to size of fish as well as depth of the habitat. Therefore, management measures probably can influence the amount of product that the fishery can produce. For example, restricting fishing to waters shallower than 458 m may provide a 4% greater fillet yield than would be the case if the

TABLE 2.—Analysis of variance for fillet yield of Dover sole as a variable and depth of capture and length as treatments. Asterisks denote $P < 0.05$.

Source	Sum of squares	df	Mean square	F
Depth > 458 m				
Seasons 2 and 3[a]	0.947	1	0.947	0.249
Fish length	32.088	5	6.418	1.641
Error[b]	262.014	67	3.911	
Depth < 458 m				
Seasons 1–4[a]	2,744.927	3	914.976	126.298*
Fish length	201.960	6	33.660	4.646*
Error[b]	963.531	133	7.245	
Depth < 458 m versus depth > 458 m				
Depth strata (season 2)	744.493	1	744.493	174.432*
Fish length	2.878	4	0.720	0.169
Error[b]	58.520	84	4.268	

[a] Seasons: 1 = April–June; 2 = July–September; 3 = October–December; 4 = January–March.

[b] Error terms include all interactions that were not significant.

entire fishery were conducted in deep water, provided that annual catch totals do not change. At 1981 prices and landings, the difference would be about $1.5 million worth of product per year to processors. To increase yield, the mesh size of trawl nets also could be altered to select for fish near 40–42 cm long, which produce the greatest fillet yield, or perhaps fishing could be directed to areas where these individuals are abundant.

Unfortunately, Dover sole are not always available in shallow waters, and fish that produce the greatest fillet yield may not be concentrated on discrete fishing grounds. Furthermore, economic gains made possible by an increased mesh size may be offset by losses in catches of shortspine thornyhead (*Sebastolobus alascanus*), longspine thornyhead (*S. altivelis*) and sablefish (*Anoplopoma fimbria*), which are usually caught together with Dover sole in deep water. In order to better gauge the economic impact of changes in mesh size, data are needed on length-frequency distributions of Dover sole, the two thornyheads, and sablefish, as well as all other species taken in the trawl fishery for Dover sole. These data need to be collected from shallow as well as deep fishing grounds.

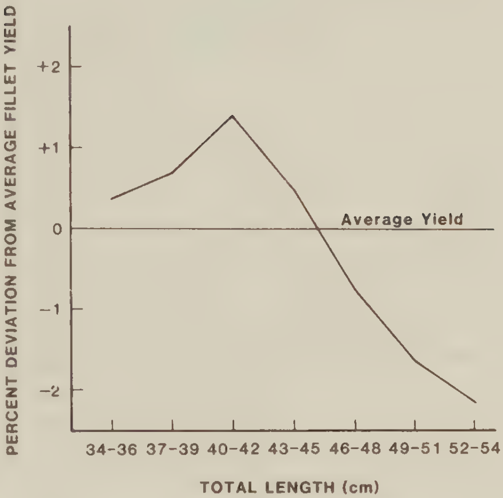

FIGURE 1.—Percent deviation of fillet yield from the average by total-length class of Dover sole caught at depths less than 458 m.

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86135

INCIDENTAL DOLPHIN MORTALITY IN THE EASTERN TROPICAL PACIFIC TUNA FISHERY, 1973 THROUGH 1978

Bruce E. Wahlen[1]

ABSTRACT

Since the late 1950's, large numbers of dolphins have been killed incidentally in the yellowfin tuna purse seine fishery in the eastern tropical Pacific. Estimates of numbers of dolphins killed incidentally in this fishery from 1973 through 1978 were made previously using a stratified ratio estimator. Previous estimates were revised by reducing the number of strata and incorporating revisions in the data. Revised estimates of total mortality, which are consistently more precise than previous estimates, declined from about 100,000 dolphins per year from 1973 through 1976 to about 25,000 and 15,000 during 1977 and 1978. The decline in estimated mortality between 1976 and 1977 was primarily the result of a decline in the kill rate which coincided with a significant management action in late 1976. Other examples during the 1964 through 1982 period of such a temporal correspondence between a change in the number or distribution of dolphins killed and legal or management actions are discussed.

Since the late 1950's, tuna purse seine fishermen operating in the eastern tropical Pacific Ocean (ETP) have exploited several dolphin species—primarily spotted dolphins, *Stenella attenuata*, and spinner dolphins, *S. longirostris*, and also striped dolphins, *S. coeruleoalba*, and common dolphins, *Delphinus delphis*—to locate and catch yellowfin tuna, *Thunnus albacares*. Perrin (1969) described the process of deploying, or setting, the net around the tuna and dolphins, and then releasing the dolphins while retaining the tuna. During this process, however, large numbers of dolphins have been killed incidentally by becoming entangled in the purse seines (Smith 1983).

The U.S. Marine Mammal Protection Act of 1972 mandated the Secretary of Commerce to make periodic assessments of the condition of dolphin populations involved in this ETP fishery. As a result of a 1976 ruling by a U.S. District Court regarding regulations promulgated under the Act, the Federal Government established annual dolphin mortality limits for the U.S. registered fleet (Fox 1978). Estimates of annual dolphin mortality have been an integral component of periodic assessments (Smith 1983).

Estimates of cumulative dolphin mortality made throughout the year are used to monitor mortalities relative to the annual limits (Lo et al. 1982). When a particular limit is reached, regulations prohibit U.S. registered vessels from fishing on the affected populations for the remainder of the year. In October 1976, the National Marine Fisheries Service (NMFS) issued a prohibition notice for the first time (Federal Register 1976), but because of litigation the notice did not become effective until November 1976.

In recent years, researchers have published several estimates and revisions of estimates of dolphin mortality incidental to this fishery. For the period 1959-78, estimates have been made by Smith (1979[2]), Lo et al. (1982), Smith (1983), and Lo and Smith (1986); for the years 1979-83, see Allen and Goldsmith (1981, 1982), Lo et al. (1982), Hammond and Tsai (1983), Hammond (1984), and Hammond and Hall (1985).

Lo et al. (1982) suggested that previous estimates of dolphin mortality incidental to this fishery were based on a stratification scheme with an unnecessarily large number of strata. In this paper, I revise the 1973-78 estimates for U.S. registered purse seiners by reducing the number of strata and by incorporating revisions in the data.

DATA

Sample data were obtained from recorded observations of scientific observers who had been placed by the NMFS aboard selected U.S. registered tuna purse seine vessels fishing in the ETP. Data recorded by these observers included the type, date,

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.

[2] Smith, T. D. (editor). 1979. Report of the status of porpoise stocks workshop, La Jolla, Calif., 27-31 August 1979. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-41, 120 p.

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location, and estimated tuna catch of each set, and other information describing the fishing operation. For sets involving dolphins (dolphin sets), the observers collected additional data, including the number of dolphins killed by species.

In 1973, all sampled trips were arranged with vessel captains under a voluntary sampling program. Beginning in 1974, trips to be sampled were determined from a randomly ordered list of vessels. Which trips were actually sampled during 1974 and 1975 depended on several factors, including the cooperation of the captains. Because of uncertainties about the cooperation of the captains and the number of fishing trips that would be made in a year, observers were placed on vessels as soon as possible. Thus, before 1976, the planned number of sampled trips was frequently obtained in the first half of the year. The sampling process became more random starting in 1976, when participation in the sampling program became mandatory for captains making sets on dolphins.

I extracted independent information for the population of all fishing trips by U.S. registered tuna purse seiners in the ETP from the Inter-American Tropical Tuna Commission (IATTC) logbook data base. This data base contains abstracts of vessels' logbooks obtained by IATTC personnel. An individual entry in the logbook data base provides information about one or more sets, including number of sets, set type, date and location, estimated tuna catch by species, but not numbers of dolphins killed.

The logbook data are incomplete in that number of sets may be missing, set type may not be recorded, and information for some sets of a trip and for all sets of some trips may be omitted (Punsly 1983). To compensate for these omissions from the logbook data, Punsly (1983) estimated the total number of dolphin sets made by all U.S. and non-U.S. seiners in the ETP. He then modified this procedure to estimate the total number of dolphin sets made by U.S. seiners only (Table 1).

METHODS

I stratified the data to allow for potential differences in dolphin kills. If kills do indeed differ among strata, then a stratified estimator may be superior to an unstratified estimator in two respects. First, a stratified estimator will have a smaller standard error and thus be more precise. Second, if the sample data are unrepresentative of the population with respect to these strata, a stratified estimator will be less biased.

Therefore, estimates of incidental dolphin mortality by species or species grouping were computed using a stratified kill-per-set ratio estimator, following the general approach described by Lo et al. (1982). I excluded trips which made no dolphin sets and experimental-gear trips from the sample and the population. However, I added dolphin kills incidental to the experimental-gear trips as constants to the mortality estimates.

I stratified the dolphin set data by four factors used in previously published estimates: 1) year of the set, 2) fish-carrying capacity of the vessel, or simply vessel capacity, 3) period within year of the set, and 4) geographic location of the set. Vessel capacity was divided into two categories—small and large. The breakpoint between categories was determined by examining the cumulative distribution of sampled trips by capacity. Periods were defined to be quarters of the year, considering the results of Wahlen and Smith (1985). The ETP was divided into three geographic areas—North Inside, North Outside, and South (Fig. 1)—because mean kill (per set) after 1978 has been shown to differ among these areas.[3]

In previous estimates, the amount of tuna caught in the set was included as a stratification factor. However, Hammond and Tsai (1983) found that stratification by this factor made very little difference in their estimates. For that reason and to avoid possible overstratification, I omitted amount of tuna caught as a stratification factor.

I pooled dolphin set data over strata when it was determined that between-strata differences in mean kill were not statistically significant or that sample sizes were otherwise too small. I prorated the estimated numbers of dolphin sets made by U.S. seiners (Table 1) among the pooled strata according to pro-

TABLE 1.—Estimated number of dolphin sets made by U.S. purse seiners fishing in the eastern tropical Pacific, by year.[1]

Year	Number of dolphin sets
1973	8,341
1974	7,475
1975	7,902
1976	7,126
1977	7,239
1978	4,214

[1] Peterson, C. L. (editor). 1984. The quarterly report October-December 1983 of the Inter-American Tropical Tuna Commission. Inter-Am. Trop. Tuna Comm., c/o Scripps Inst. Oceanogr., La Jolla, CA 92093.

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[3] K.-T. Tsai, Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92093, pers. commun. December 1983.

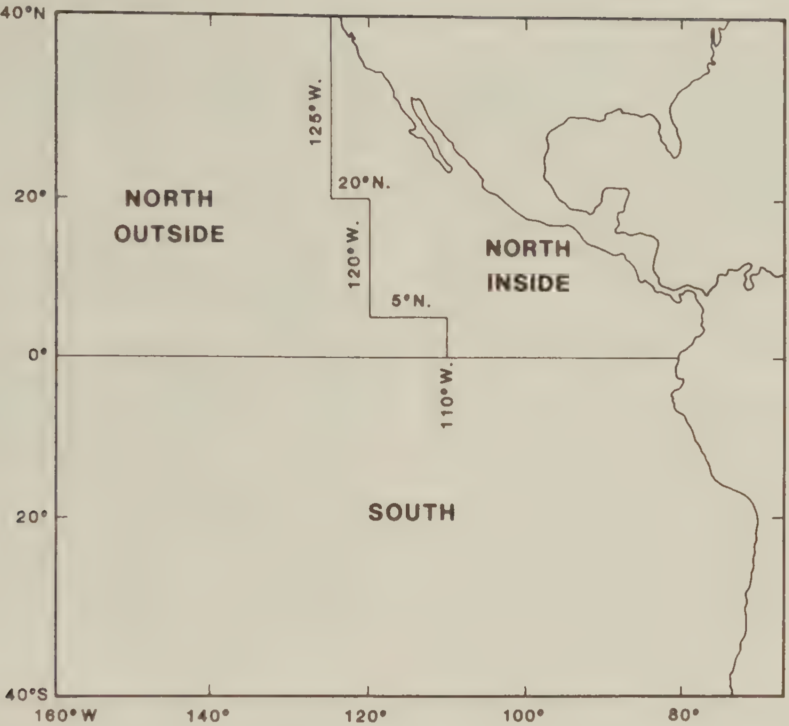

FIGURE 1.—The three areas of the eastern tropical Pacific used to stratify the data, bounded by lat. 40°N, long. 160°W, lat. 40°S, and the western coastline of the North and South American continents.

portions of known dolphin sets which were calculated from logbook data.

I tested for significant between-strata differences in mean total kill using analysis of variance (ANOVA) methods of BMDP programs P7D and P2V (Dixon 1983). Violation of the ANOVA assumption of equal cell variances may seriously distort significance probabilities in unbalanced models such as in this study (Glass et al. 1972). Because such distortion could be great, test results were considered to be inconclusive when significance probabilities were close to 0.05.

I was unable to test for the combined effect of all four stratification factors using the whole data set because data were sparse or unavailable in many of the 144 cells of the proposed four-factor stratification. Thus, ANOVA results for restricted subsets of the data containing adequate sample sizes were assumed to hold for subsets with inadequate sample sizes. To eliminate significant between-factor interactions, I tried logarithmic and power transformations of the dependent variable, total number of dolphins killed. When these transformations failed to eliminate the interactions, I partitioned the analysis into individual levels of the interacting variables.

When it was necessary to determine where the within-factor differences occurred, t-tests for differences between all pairs of cell means were made. Since I tested for differences between all pairs rather than between a few preselected pairs, a difference was considered significant if its significance probability was less than the quotient of 0.05 and the number of pairs. This Bonferroni adjustment to the significance level of each test assured a level of 0.05 simultaneously across all tests (Snedecor and Cochran 1980).

I computed t-values for pairwise differences using separate rather than pooled variance estimates because the cell variances were unequal according to Levene's test; this test was selected because it is more robust under nonnormality than either the common F-ratio or Bartlett's test (Brown and Forsythe 1974). Degrees of freedom were calculated with Satterthwaite's approximation, so that significance probabilities could be obtained from an ordinary t-distribution (Snedecor and Cochran 1980).

RESULTS

Setting the breakpoint between small and large vessel capacities at 600 tons (or lower) or at 1,200 tons would, in each case, create small and large vessel categories with severely unbalanced sample sizes (Table 2). The percent of sampled vessels with capacity <1,000 tons was more stable over years than the percent of sampled vessels <800 tons, especially from 1973 through 1976. Therefore, the breakpoint between vessel categories was set at 1,000 tons.

Because of data sparseness, particularly in the North Outside and South areas (Table 3), I made three multiway ANOVA tests restricted to subsets of the whole data set: 1) two-way test of year and vessel capacity, restricted to the North Inside area and the second quarter, 2) three-way test of year, quarter, and vessel capacity, restricted to the North Inside area and the first two quarters during 1973 through 1976, and 3) four-way test, restricted to the North Inside and North Outside areas, and the

TABLE 2.—Cumulative distributions of number of sampled U.S. purse seine trips, by vessel capacity (tons) for the years 1973-78, with relative frequencies (percents) in parentheses.

Vessel capacity (tons)	Year					
	1973	1974	1975	1976	1977	1978
<200	0	0	0	0	0	0
	(0)	(0)	(0)	(0)	(0)	(0)
<300	0	1	1	0	0	0
	(0)	(3)	(3)	(0)	(0)	(0)
<400	1	3	2	3	0	0
	(4)	(8)	(7)	(7)	(0)	(0)
<600	5	9	5	11	15	8
	(22)	(24)	(17)	(24)	(15)	(8)
<800	15	15	8	20	34	27
	(65)	(41)	(28)	(43)	(35)	(26)
<1,000	16	20	16	24	39	33
	(70)	(54)	(55)	(52)	(40)	(32)
<1,200	20	30	26	34	70	67
	(87)	(81)	(90)	(74)	(71)	(66)
Total	23	37	29	46	98	102
	(100)	(100)	(100)	(100)	(100)	(100)

TABLE 3.—Number of dolphin sets made during sampled trips, by year, vessel capacity (tons), quarter of the year, and area.

Year	Vessel capacity (tons)	Quarter	Area			Total
			North Inside	North Outside	South	
1973	<1,000	1	325	0	9	334
		2	167	47	0	214
		3	0	0	0	0
		4	0	0	0	0
		Total	492	47	9	548
	≥1,000	1	116	0	5	121
		2	43	2	0	45
		3	0	0	0	0
		4	0	0	0	0
		Total	159	2	5	166
1974	<1,000	1	459	0	0	459
		2	88	0	0	88
		3	0	6	0	6
		4	0	0	0	0
		Total	547	6	0	553
	≥1,000	1	362	0	0	362
		2	57	0	0	57
		3	31	12	0	43
		4	0	0	0	0
		Total	450	12	0	462
1975	<1,000	1	404	0	3	407
		2	106	0	4	110
		3	0	0	0	0
		4	0	0	0	0
		Total	510	0	7	517
	≥1,000	1	268	0	0	268
		2	111	0	5	116
		3	47	0	0	47
		4	0	0	0	0
		Total	426	0	5	431
1976	<1,000	1	155	0	0	155
		2	41	27	0	68
		3	18	71	0	89
		4	20	13	4	37
		Total	234	111	4	349
	≥1,000	1	129	0	118	247
		2	42	0	0	42
		3	17	80	1	98
		4	16	6	0	22
		Total	204	86	119	409
1977	<1,000	1	3	0	1	4
		2	239	67	0	306
		3	433	134	0	567
		4	53	0	0	53
		Total	728	201	1	930
	≥1,000	1	0	0	2	2
		2	563	86	16	665
		3	1,034	218	23	1,275
		4	356	30	31	417
		Total	1,953	334	72	2,359
1978	<1,000	1	170	0	13	183
		2	75	50	0	125
		3	86	138	0	224
		4	59	6	0	65
		Total	390	194	13	597
	≥1,000	1	320	0	52	372
		2	117	77	1	195
		3	104	255	2	361
		4	165	8	15	188
		Total	706	340	70	1,116
Total			6,799	1,333	305	8,437

second and third quarters during 1977 and 1978. Additionally, pairwise t-tests were made to isolate annual and quarter differences detected by the above tests.

Tests for Year Differences

Sample statistics of mean kill by year and vessel capacity (Test 1) revealed an unbalanced design and suggested that cell variances were related to cell means (Table 4). For each of several transformations of total kill, neither the interaction between vessel capacity and year nor the difference between vessel capacities was significant, but the difference among years was significant.

To determine where the yearly differences occurred, the data were pooled over vessel capacity so that t-tests for differences between each pair of yearly means could be made. The resulting one-way classification by year was unbalanced and characterized by significantly different cell variances ($P < 0.001$), and suggested that the means from 1973 through 1976 were larger than the means from 1977 and 1978 (Table 4).

Results from pairwise t-tests indicated that means were not significantly different within each of the two periods from 1973 through 1976 and from 1977 through 1978 (Table 5). However, each of the means from 1973 through 1976 was significantly different (or nearly so) from each of the means from 1977 and 1978 (Table 5). Based on these results, I divided the data into two periods, 1973 through 1976 and 1977 through 1978, for further tests within each period.

Tests for Differences Within the 1973-76 Period

The three-way ANOVA table by year, quarter, and vessel capacity (Test 2) was unbalanced and suggested that cell variances were unequal (Table 6). Furthermore, no between-factor interactions were significant. The test for year differences was inconclusive; however, there is evidence for a year effect within only one cell (1976, quarter 1, small vessels), and there is no consistent yearly pattern of means within rows of the table. Therefore, I concluded that annual means during 1973-76 were not significantly different and, hence, I pooled over years within this period. I also pooled over vessel capacity since it was not a significant effect during these years.

Before 1976, sample data were unrepresentative of quarter and area, since nearly all data were obtained from trips made during the first half of the year and, thus, within the North Inside area. Data sparseness in the North Outside and South areas,

TABLE 4.—Mean of total number of dolphins killed ($\bar{k}$), standard deviation (s), and number of dolphin sets (d) for sampled trips, by year and vessel capacity (tons) for all sets made in the North Inside area during quarter two. Significance probabilities (P) obtained for 2-way ANOVA's on transformed values of total kill: interaction ($P \geqslant 0.1180$), year ($P < 0.001$), and vessel capacity ($P \geqslant 0.7851$).

Vessel capacity (tons)	Statistic	Year					
		1973	1974	1975	1976	1977	1978
<1,000	$\bar{k}$	8.62	6.20	16.33	8.58	3.08	2.35
	s	18.84	10.94	40.73	20.08	11.64	7.34
	d	167	88	106	41	239	75
≥1,000	$\bar{k}$	11.49	5.25	8.79	14.57	2.53	1.18
	s	25.96	14.08	17.43	32.44	7.84	3.31
	d	43	57	111	42	563	117
Pooled	$\bar{k}$	9.21	5.83	12.47	11.61	2.69	1.64
	s	20.46	12.23	31.23	27.05	9.13	5.28
	d	210	145	217	83	802	192

TABLE 5.—Matrix of significance probabilities associated with t-tests for differences between pairs of annual means of total number of dolphins killed. Significant values, required by the Bonferroni adjustment to be <0.0033, are indicated by "*", and nearly significant values are indicated by "+". Data are from sampled dolphin sets made during quarter two in the North Inside area.

Year	Year				
	1974	1975	1976	1977	1978
1973	0.0526	0.2007	0.4659	0.0000^{*}	0.0000^{*}
1974		0.0050	0.0681	0.0037^{+}	0.0002^{*}
1975			0.8139	0.0000^{*}	0.0000^{*}
1976				0.0037^{+}	0.0013^{*}
1977					0.0344

TABLE 6.—Mean of total number of dolphins killed ($\bar{k}$), standard deviation (s), and number of dolphin sets (d) for sampled trips, by year, quarter, and vessel capacity (tons) for all sets made in the North Inside area during the first two quarters of 1973-76. Significance probabilities (P) obtained for a 3-way ANOVA on total kill: interactions ($P \geqslant 0.1374$), year ($P = 0.0534$), quarter ($P = 0.0501$), and vessel capacity ($P = 0.8219$).

Vessel capacity (tons)	Quarter	Statistic	Year			
			1973	1974	1975	1976
<1,000	1	$\bar{k}$	23.15	14.10	16.45	3.47
		s	69.70	40.39	47.31	8.12
		d	325	459	404	155
	2	$\bar{k}$	8.62	6.20	16.33	8.59
		s	18.84	10.94	40.73	20.08
		d	167	88	106	41
≥1,000	1	$\bar{k}$	15.75	11.23	15.45	10.86
		s	27.64	24.85	34.37	24.35
		d	116	362	268	129
	2	$\bar{k}$	11.49	5.25	8.79	14.57
		s	25.95	14.08	17.43	32.44
		d	43	57	111	42

resulting from the unrepresentative areal sample, precluded testing for an area effect during the 1973-76 period (Table 3); however, after 1978 mean kills were shown to differ among the three areas, as noted earlier. Therefore, to minimize the amount of bias which might be introduced into the estimates from a sample which was unrepresentative of area, I retained the three-area stratification.

Small sample sizes during 1973-76 dictated pooling over all quarters within both the North Outside and South areas and over quarters 3 and 4 within the North Inside area (Table 3). The test result for quarter 1 and 2 differences in the North Inside area was inconclusive (Table 6). Based on bias considerations similar to those above, I did not pool data from quarters 1 and 2 in the North Inside area in case their means did indeed differ.

After pooling over year, vessel capacity, and quarter as indicated above, five strata remained for the 1973-76 data: 1) North Inside, quarter 1, 2) North Inside, quarter 2, 3) North Inside, quarters 3 and 4 pooled, 4) North Outside, all quarters pooled, and 5) South, all quarters pooled.

Tests for Differences Within the 1977-78 Period

Interpretation of the four-way ANOVA (Test 3), restricted by data sparseness to the North Inside and North Outside areas during the second and third quarters of 1977-78 (Table 3), was complicated by significant interaction between quarters and each of the other three factors ($P \leqslant 0.0159$, for total kill and all transformations of total kill). Therefore, the four-way table was partitioned into two, three-way tables, one for each level of quarter (Tables 7, 8), and decisions about between-strata differences during these years were based on results obtained separately for each quarter.

For second quarter data, interactions were not significant (Table 7). However, for third quarter data, interaction between year and vessel capacity was significant ($P < 0.001$) primarily because of the two large means recorded in the North Inside and North Outside areas by small vessels during 1978 (Table 8). Omitting the data from one extraordinarily large kill set in each of these two cells reduces their means from 11.27 to 4.68 for the North Inside and from 9.77 to 5.46 for the North Outside.

Results from the second and third quarter data were inconsistent for both year and vessel capacity. Neither effect was significant during the second quarter (Table 7), but during the third quarter (Table 8) the large means in the two cells noted above provided some evidence of both a year and vessel capacity effect. Since the evidence for both a year and vessel capacity effect was confined to two, third quarter cells whose means were each strongly influenced by only one set, I concluded that year and vessel capacity were not significant effects during 1977-78. Hence, I pooled over year and vessel capacity within this period. The evidence regarding an area effect during 1977-78 was also inconsistent between quarters (Tables 7, 8); however, I retained area as a stratification factor since it was shown to be significant after 1978.

Beginning in 1976 when the sampling program became mandatory the sample data became more representative of quarter. Thus, for the 1977-78 data, bias considerations were of lesser importance

TABLE 7.—Mean of total number of dolphins killed ($\bar{k}$), standard deviation (s), and number of dolphin sets (d) for sampled trips, by area, vessel capacity (tons), and year for all sets made in the North Inside and North Outside areas during quarter two of 1977-78. Significance probabilities (P) obtained for a 3-way ANOVA on total kill: interactions ($P \geqslant 0.2095$), area ($P = 0.0060$), vessel capacity ($P = 0.8857$), and year ($P = 0.6050$).

Year	Vessel capacity (tons)	Statistic	Area	
			North Inside	North Outside
1977	<1,000	$\bar{k}$	3.08	2.94
		s	11.64	8.68
		d	239	67
	≥1,000	$\bar{k}$	2.53	5.66
		s	7.84	13.82
		d	563	86
1978	<1,000	$\bar{k}$	2.35	4.82
		s	7.34	16.00
		d	75	50
	≥1,000	$\bar{k}$	1.18	4.26
		s	3.31	21.19
		d	117	77

TABLE 8.—Mean of total number of dolphins killed ($\bar{k}$), standard deviation (s), and number of dolphin sets (d) for sampled trips, by area, vessel capacity (tons), and year for all sets made in the North Inside and North Outside areas during quarter three of 1977-78.

Year	Vessel capacity (tons)	Statistic	Area	
			North Inside	North Outside
1977	<1,000	$\bar{k}$	2.08	2.33
		s	5.72	7.92
		d	433	134
	≥1,000	$\bar{k}$	2.85	2.89
		s	9.81	6.45
		d	1034	218
1978	<1,000	$\bar{k}$	11.27	9.77
		s	61.74	52.52
		d	86	138
	≥1,000	$\bar{k}$	2.00	2.81
		s	4.34	10.97
		d	104	255

in stratification decisions than for the 1973-76 data. The four-way test on 1977-78 data (Test 3) was not helpful in resolving the question of quarter differences because of the interactions between quarter and each of the other three factors. However, pairwise t-tests for differences between quarterly means in the North Inside area during 1977-78, pooled over year and vessel capacity, detected no significant quarter differences (Table 9). Based on that result, I pooled over all quarters in the North Inside and North Outside areas. Finally, I pooled over all quarters in the South area because of the small sample sizes (Table 3).

TABLE 9.—Matrix of significance probabilities associated with t-tests for differences between pairs of quarterly means of total number of dolphins killed. No significant values, required by the Bonferroni adjustment to be <0.0083, were attained. Data are from sampled dolphin sets made in the North Inside area from 1977 through 1978.

	Quarter		
Quarter	2	3	4
1	0.7062	0.2417	0.0684
2		0.2623	0.0730
3			0.2831

Thus, after pooling over year, vessel capacity, and quarter as indicated above, only three strata remained for the 1977-78 data: 1) North Inside, 2) North Outside, and 3) South.

Estimates

I obtained annual estimates of the total number of dolphins killed by summing estimates for each of three or five strata, depending on the year. Estimates for a stratum were computed as the product of (a) total number of dolphin sets (Table 10) and (b) the corresponding total kill-per-set ratio (Table 11), increased by (c) the observed total number of dolphins killed during experimental-gear trips (Table

TABLE 10.—Estimated number of dolphin sets (D) and number of trips (N) for the population of trips, by year within strata.

		North Inside						
Year	Statistic	Quarter 1	Quarter 2	Quarters 3 & 4	Total	North Outside	South	Total
1973	D	3,203	1,670	501		2,591	330	8,295
	N	172	104	69		117	34	
1974	D	3,486	1,176	242		2,453	12	7,369
	N	126	92	38		93	4	
1975	D	3,069	1,749	434		2,495	53	7,800
	N	119	96	40		96	23	
1976	D	1,618	1,520	716		2,001	729	6,584
	N	127	98	92		90	76	
1977	D				5,722	1,128	252	7,102
	N				186	76	37	
1978	D				2,811	1,153	162	4,126
	N				206	58	27	

TABLE 11.—By-trip means of total number of dolphins killed ($\bar{k}$) and of number of dolphin sets ($\bar{d}$), total kill-per-set ratio ($\hat{R}$), estimated standard error of the total kill-per-set ratio (s), and number of sampled trips (n), by strata.

		North Inside					
Years	Statistic	Quarter 1	Quarter 2	Quarters 3 & 4	Total	North Outside	South
1973-76	$\bar{k}$	354.51	157.32	155.50		265.06	239.85
	$\bar{d}$	24.11	15.98	9.31		16.50	7.45
	$\hat{R}$	14.70	9.85	16.70		16.06	32.19
	s	1.19	1.15	4.38		4.21	4.17
	n	92	41	16		16	20
1977-78	$\bar{k}$				58.66	57.55	22.12
	$\bar{d}$				19.88	13.71	4.73
	$\hat{R}$				2.95	4.20	4.68
	s				0.23	0.51	1.03
	n				190	78	33

12). For example, the total estimated kill for 1977 (Table 13) was obtained as a sum of estimates of the total for three strata as [(5,722)(2.95) + 175] + [(1,128)(4.20) + 15] + [(252)(4.68) + 0]. Estimates for each species or species grouping were obtained in the same manner as estimates of the total, except that values for the species or species grouping were substituted for the totals in (b) and (c) above.

Similarly, I estimated the variance of the number of dolphins killed during any year by summing variance estimates for each stratum. The estimated variance of total kill for a stratum was computed

TABLE 12.—Total number of dolphins killed (*k*), number of dolphin sets (*d*), and number of experimental-gear trips (*n*), by year within strata. These data were excluded from all sample and population statistics.

		North Inside						
Year	Statistic	Quarter 1	Quarter 2	Quarters 3 & 4	Total	North Outside	South	Total
1973	*k*	0	0	513		0	0	513
	d	0	0	46		0	0	46
	n	0	0	2		0	0	
1974	*k*	0	0	497		192	0	689
	d	0	0	70		36	0	106
	n	0	0	2		1	0	
1975	*k*	0	0	512		271	0	783
	d	0	0	76		26	0	102
	n	0	0	2		1	0	
1976	*k*	139	1,400	111		1,886	547	4,083
	d	35	256	92		153	6	542
	n	2	16	7		5	2	
1977	*k*				175	15	0	190
	d				129	8	0	137
	n				4	2	0	
1978	*k*				226	27	0	253
	d				77	11	0	88
	n				6	2	0	

TABLE 13.—Estimates of dolphin mortality incidental to U.S. purse seiners, by species grouping and year, with coefficients of variation in parentheses.

	Year					
Species grouping	1973	1974	1975	1976	1977	1978
Spotted	70,000 (0.12)	61,000 (0.13)	63,000 (0.13)	61,000 (0.11)	14,000 (0.08)	9,000 (0.08)
Spinner						
Eastern[1]	12,000 (0.16)	11,000 (0.11)	11,600 (0.11)	9,500 (0.12)	1,300 (0.12)	700 (0.11)
Whitebelly	20,000 (0.17)	16,000 (0.19)	17,000 (0.19)	19,000 (0.15)	3,600 (0.11)	2,300 (0.10)
Unidentified	8,700 (0.24)	7,600 (0.26)	7,700 (0.25)	7,500 (0.25)	60 (0.18)	40 (0.17)
Total	41,000	35,000	36,000	36,000	5,000	3,000
Common	8,500 (0.22)	7,000 (0.25)	8,300 (0.22)	6,600 (0.20)	3,000 (0.23)	1,500 (0.24)
Striped	640 (0.30)	380 (0.34)	500 (0.35)	800 (0.33)	200 (0.26)	130 (0.24)
Unidentified	5,000 (0.19)	3,700 (0.20)	4,000 (0.19)	5,400 (0.26)	450 (0.12)	300 (0.12)
Other	180 (0.45)	90 (0.26)	100 (0.26)	280 (0.64)	180 (0.22)	100 (0.26)
Total[2]	125,000 (0.10)	107,000 (0.10)	112,000 (0.10)	110,000 (0.09)	23,000 (0.06)	14,000 (0.06)

[1] May include small number of Costa Rican spinner dolphins.

[2] Sum of estimated kills over species grouping not exactly equal to total estimated kill because of rounding error.

as the square of the product of (a) the number of dolphin sets[4] (Table 10) and (b) the corresponding estimated standard error of the total kill-per-set ratio (Table 11). I computed the estimated stratum variance for each species or species grouping, substituting values for the species or species grouping for the total in (b) above. I estimated the standard errors (Table 11) using mean number of dolphin sets per trip calculated from the sample rather than from the population (Lo et al. 1982).

My annual estimates of the total number of dolphins killed incidentally in the U.S. purse seine fishery of the ETP ranged from a maximum of 125,000 dolphins in 1973 to a minimum of 14,000 dolphins in 1978, with coefficients of variation (CV) no greater than 10% (Table 13). The estimated mortalities of the two species most often exploited, spotted and spinner dolphins, together accounted for about 80-90% of each annual total.

DISCUSSION AND CONCLUSIONS

The kill-per-set ratio, or mean kill, declined from 15 dolphins/set during the 1973-76 period to 3 dolphins/set during the 1977-78 period (Table 11, pooled over quarter and area). Many changes affecting dolphin kill were made during these periods, including improvements in fishing gear and dolphin-release procedures and introduction of federal regulations. The change in mean kill between 1973-76 and 1977-78 coincided with the first NMFS notice in late 1976 prohibiting fishing on dolphins for the remainder of the year. This one example of a correspondence between a change in the number or distribution of dolphins killed during purse seine sets and an identifiable legal or management action is not necessarily indicative of a cause and effect relationship. There are, however, two other examples of such a temporal correspondence present in the data from 1964 through 1982.

In the second example, the data prior to 1973, while sparse, suggest that the mean kill was substantially higher than during the 1973-76 period. Lo and Smith (1986) reported a mean kill of 46 dolphins/set based on 1964 through 1972 data, pooled over vessel capacity and catch of tuna. They found no consistent differences in annual mean kill during that period. The decline in the mean from 46 dolphins/set during the 1964-72 period to 15 dolphins/set during the 1973-76 period coincided with the passage of the Marine Mammal Protection Act in late 1972.

In the third example, Wahlen and Smith (1985) demonstrated a difference between the two periods from 1979 through March 1981 and from April 1981 through 1982 in the frequency distributions of number of dolphins killed during purse seine sets. While the difference in mean kill during these two periods was not significant, the percent of dolphin sets in which no dolphins were killed (zero-kill sets) decreased significantly. This decrease coincided with a court order in March 1981 which prohibited using data collected by NMFS observers to monitor compliance of vessel captains with dolphin-release procedures.

These three examples suggest that significant legal or management actions can affect kill rates, measured by the kill-per-set ratio or by the percent of zero-kill sets. Furthermore, such effects on the kill-per-set rate are reflected in the series of estimates of total numbers of dolphins killed presented here. For example, between 1976 and 1977 the number of dolphin sets increased slightly (Table 10), yet total estimated mortality decreased by nearly 80% (Table 13), due primarily to the significantly lower kill rate after 1976. The further decline in estimated mortality to 14,000 dolphins in 1978 reflects both the lower kill rate and a decline in the number of dolphin sets. Thus, the decrease in the kill rate following the first enforcement of dolphin kill limits in 1976 is reflected in the decrease in the estimates of total mortality after 1976.

My estimates of total annual dolphin mortality in U.S. purse seine fishing from 1973 through 1978 (Table 13) are lower, except for 1976, and more precise than those in the Status of Porpoise Stocks Workshop Report (SOPS) (Table 14). However, for each year except 1973, my estimated total is contained inside an approximate 95% confidence interval around the estimated total ($\hat{T}$) in SOPS, where the confidence interval is computed as $\hat{T} \pm 2 \cdot \mathrm{CV} \cdot \hat{T}$. Thus, the differences between my point estimates and those in SOPS are small when the imprecision (large CV) of the SOPS estimates is considered.

The lower precision of the SOPS estimates may be due to overstratification because of a concern that the sample might not be representative of the population, particularly during the 1973-75 period. Thus, in order to minimize bias, a large number of strata (32 per year) were defined. Tests for between-strata differences in mean kill were not made, but strata were pooled to the degree that each pooled stratum contained some sample data. However, even after pooling, some strata during the years 1973-76

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[4] Numbers of dolphin sets were treated as constants since no variances were provided for these estimated quantities. Therefore, my variances of estimated mortality are underestimated to an unknown, though likely small, degree.

TABLE 14.—Estimates of dolphin mortality incidental to U.S. purse seiners, by species and year, from Status of Porpoise Stocks Workshop Report (Smith text footnote 2). Coefficients of variation of totals in parentheses.

	Year					
Species	1973	1974	1975	1976	1977	1978
Spotted	114,000	75,000	84,000	57,000	12,000	13,000
Spinner	65,000	62,000	70,000	39,000	5,000	4,400
Common	18,000	3,000	2,300	5,400	6,600	1,000
Striped	40	140	900	2,000	100	250
Unidentified[1]	0	0	0	0	0	0
Other	0	80	160	690	80	50
Total[2]	197,000 (0.17)	140,000 (0.41)	157,000 (0.17)	104,000 (0.13)	24,000 (0.15)	19,000 (0.20)

[1] Kills of unidentified dolphins prorated among known species.

[2] Sum of estimated kills over species not exactly equal to total estimated kill because of rounding error.

contained only one dolphin set. Such small sample sizes within some strata account for the lower precision of the SOPS estimates relative to my estimates.

While the differences between my point estimates and those in SOPS are small in a statistical sense, my estimates are consistently lower except for 1976. However, these new estimates are to be preferred on methodological grounds. I tested for statistically significant between-strata differences in mean kill and pooled over strata when significant differences were not detected or when sample sizes were otherwise too small. Pooling of the data produced estimates which were more precise than the SOPS estimates because it resulted in fewer strata with larger sample sizes. However, to minimize the possibility of introducing bias into the estimates during the 1973-76 period, when the sample was unrepresentative of area and quarter, I did not pool over area and I pooled over quarter only in the event of small sample sizes.

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Composition of the Incidental Kill of Small Cetaceans in the US Purse–Seine Fishery for Tuna in the Eastern Tropical Pacific, 1982 through 1984

Bruce E. Wahlen, G. Jay Walker, Ruth B. Miller and Charles W. Oliver

Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, USA

ABSTRACT

Composition of the small cetacean incidental kill by US registered purse–seiners fishing in the eastern tropical Pacific from 1982 to 1984 is reported by area, species, stock, sex, length and reproductive condition. The data were collected by Inter-American Tropical Tuna Commission and National Marine Fisheries Service technicians placed aboard a total of 162 vessel-trips made during these three years. Differences between the data treatment here as opposed to that in two previous papers are discussed.

INTRODUCTION

Several papers describing the small cetacean kill incidental to fishing activities of tuna purse-seiners in the eastern tropical Pacific (ETP) have been published, including Lo, Powers and Wahlen (1982), Perrin and Oliver (1982), Hammond and Tsai (1983), Oliver, Walker and Miller (1983), Smith (1983), Hammond (1984), Hammond and Hall (1985) and Wahlen and Smith (1985). Forthcoming papers include Lo and Smith (1986) and Wahlen (1986).

In this third in a series of papers (Perrin and Oliver, 1982; Oliver *et al.*, 1983), we report the incidental kill of small cetaceans by US registered vessels in the ETP from 1982 to 1984. These kills are classified by area, species, stock, sex, length and reproductive condition. Species represented in this report are: spotted dolphins, *Stenella attenuata*; spinner dolphins, *S. longirostris*; striped dolphins, *S. coeruleoalba*; common dolphins, *Delphinus delphis*; rough-toothed dolphins, *Steno bredanensis*; bottlenose dolphins, *Tursiops truncatus*; and short-finned pilot whales, *Globicephala macrorhynchus*.

DATA

Incidental kill data were collected by Inter-American Tropical Tuna Commission (IATTC) and National Marine Fisheries Service (NMFS) technician-observers placed aboard a sample of US registered tuna purse–seine vessels fishing in the ETP (Lo *et al.*, 1982). However, data collected aboard US registered tuna seiners chartered by non-US companies were not available to us.

Kills by area, species, stock and sex, if determined, were obtained from the 'tally' databases. Length frequencies by sex, and reproductive condition information for females, were obtained from the 'life history' databases containing extensive biological data for those dead animals which were available for 'hands-on' inspection by the technicians. The life history databases thus contain biological data for only a subset of the animals reported as killed in the tally databases, since technicians are unable to physically examine each animal killed. See Perrin and Oliver (1982) for detailed descriptions of data recorded in these databases.

Whereas in the two previous papers in this series, tally data from IATTC technicians were not included, they are included here. As in the previous papers, life history data from both IATTC and NMFS technicians are included.

METHODS

To reduce the size of the report, we have eliminated stratification by month and quarter and have reported kills down to the level of stocks only for spotted and spinner dolphins. We allocated kills of offshore spotted and whitebelly spinner dolphins to geographic stocks as in Perrin and Oliver (1982). Laboratory procedures for processing specimens and determining sexual maturity are referenced in Perrin and Oliver (1982), as is the methodology of the computer programs used to summarize the reproductive condition data.

RESULTS

Kill data from 85 trips in 1982, from 47 trips in 1983, and from 30 trips in 1984 (Table 1) are summarized by year, stock, sex and area for spotted dolphins (Table 2) and spinner dolphins (Tables 3–5), and by year, sex and area

Table 1

Number of fishing trips by US seiners which were observed by IATTC or NMFS technicians, by year and observer type. IATTC and NMFS totals are subdivided according to departure date of trips (previous year, current year). Numbers in parentheses indicate number of trips in which some dolphins were killed

Observer type		1982	1983	1984
IATTC	Previous year	6	7	3
	Current year	40	30	16
	Total	46 (39)	37 (35)	19 (18)
NMFS	Previous year	7	10	0
	Current year	32	0[1]	11
	Total	39 (37)	10 (6)	11 (11)
Total		85 (76)	47 (41)	30 (29)

[1] NMFS technicians were not placed aboard any fishing vessels which departed during 1983 because of a court order forbidding placement of NMFS technicians without a search warrant.

Table 2

Total kill of spotted dolphins by observed US vessels, by year, stock, sex (M = male, F = female), and 5 degree block number. Reported kills of 1 male offshore spotted dolphin of unknown stock and of 59 unidentified spotted dolphins during 1982, and of 1 male coastal spotted dolphin during 1983 are not included. No kills were reported for the coastal stock during 1982 and 1984. T = total

	1982						1983						1984					
	Northern offshore			Southern offshore			Northern offshore			Southern offshore			Northern offshore			Southern offshore		
5 block	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T
23	0	0	0	0	1	3	0	0	0	39	22	97	0	0	0	0	0	1
24	0	0	0	14	17	84	0	0	0	9	16	38	0	0	0	26	37	84
25	0	0	0	2	0	2	0	0	0	3	6	24	0	0	0	1	0	3
26	0	0	0	0	0	0	0	0	0	9	13	56	0	0	0	0	0	0
43	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	6	9	23	0	0	0	11	23	73	0	0	0	7	3	55
45	0	0	0	47	75	727	0	0	0	7	12	27	0	0	0	2	6	29
46	0	0	0	22	32	124	0	0	0	40	53	156	0	0	0	0	0	0
47	0	0	0	0	2	14	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0
63	8	7	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64	3	4	7	2	3	11	0	0	3	1	6	35	0	0	0	0	0	0
65	22	20	91	15	26	62	0	0	4	0	0	1	0	0	0	0	0	1
66	12	13	39	5	10	54	1	1	7	14	9	118	0	0	0	0	0	0
67	0	0	0	1	9	30	0	0	0	3	3	16	0	0	0	0	0	0
68	0	0	0	3	8	205	0	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	16	29	107	0	0	0	0	0	0	0	0	0	0	0	0
70	5	4	48	21	32	104	0	0	0	0	0	0	0	0	0	0	0	0
83	3	12	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84	1	2	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
85	23	28	228	0	0	0	0	1	1	0	0	0	0	0	10	0	0	0
86	16	23	75	0	0	0	5	14	49	0	0	0	0	3	5	0	0	0
87	1	4	9	0	0	0	0	0	0	0	0	0	13	21	150	0	0	0
88	0	0	7	0	0	0	3	2	10	0	0	0	9	14	69	0	0	0
89	1	4	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	34	64	223	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0
91	38	39	521	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	2	4	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	1	17	0	0	0	1	1	3	0	0	0	0	0	0	0	0	0
104	4	7	252	0	0	0	0	1	17	0	0	0	4	5	11	0	0	0
105	42	67	368	0	0	0	13	10	41	0	0	0	0	2	4	0	0	0
106	136	157	753	0	0	0	4	5	17	0	0	0	32	52	139	0	0	0
107	17	22	185	0	0	0	2	1	117	0	0	0	67	95	239	0	0	0
108	6	13	100	0	0	0	0	1	2	0	0	0	18	17	141	0	0	0
109	3	4	16	0	0	0	3	3	7	0	0	0	0	0	0	0	0	0
110	7	14	41	0	0	0	1	0	1	0	0	0	14	20	34	0	0	0
111	20	18	157	0	0	0	0	1	2	0	0	0	28	20	65	0	0	0
112	7	10	105	0	0	0	2	2	5	0	0	0	41	37	147	0	0	0
113	19	14	136	0	0	0	9	7	16	0	0	0	9	7	16	0	0	0
114	40	35	146	0	0	0	8	9	20	0	0	0	20	27	49	0	0	0
115	0	0	0	0	0	0	5	2	9	0	0	0	0	0	0	0	0	0
125	29	27	144	0	0	0	0	0	0	0	0	0	7	12	97	0	0	0
126	13	13	255	0	0	0	0	0	9	0	0	0	0	5	5	0	0	0
127	5	9	77	0	0	0	1	2	4	0	0	0	2	2	20	0	0	0
128	8	14	67	0	0	0	12	24	75	0	0	0	34	30	85	0	0	0
129	32	32	191	0	0	0	10	13	42	0	0	0	2	2	10	0	0	0
130	3	2	7	0	0	0	9	4	22	0	0	0	3	0	3	0	0	0
131	8	3	24	0	0	0	25	20	114	0	0	0	26	40	92	0	0	0
132	0	2	88	0	0	0	5	18	92	0	0	0	50	81	287	0	0	0
133	20	22	122	0	0	0	2	6	39	0	0	0	19	27	272	0	0	0
134	0	1	3	0	0	0	1	0	3	0	0	0	2	7	104	0	0	0
135	1	2	3	0	0	0	1	1	9	0	0	0	0	0	0	0	0	0
146	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
147	11	21	72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
148	1	1	17	0	0	0	2	6	27	0	0	0	0	0	5	0	0	0
149	0	0	13	0	0	0	1	0	10	0	0	0	0	1	3	0	0	0
151	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
168	0	0	0	0	0	0	3	1	6	0	0	0	0	0	0	0	0	0
T	601	740	4687	154	254	1556	129	157	789	136	163	641	400	527	2062	36	46	173

Table 3

Total kill of spinner dolphins by observed US vessels during 1982, by stock, sex (M = male, F = female), and 5 degree block number. Reported kill of 39 unidentified spinner dolphins is not included. No kills were reported for the Costa Rican stock

	Eastern			Northern whitebelly			Southern whitebelly		
5° block	M	F	Total	M	F	Total	M	F	Total
23	0	0	0	0	0	0	0	1	2
24	0	0	0	0	0	0	2	2	6
25	0	0	0	0	0	0	2	2	10
44	0	0	0	0	0	0	1	2	28
45	0	0	0	0	0	0	28	31	410
46	0	0	0	0	0	0	5	4	19
64	0	0	0	0	0	0	4	3	104
65	0	0	0	0	0	0	6	4	17
66	0	0	0	0	0	0	5	5	64
67	0	0	0	0	0	0	0	0	4
68	0	0	0	0	0	0	1	2	44
69	0	0	0	0	0	0	1	4	7
70	0	0	0	0	0	0	1	1	11
85	0	0	0	6	12	30	0	0	0
86	0	0	0	0	1	2	0	0	0
87	0	0	0	9	3	14	0	0	0
88	0	0	0	1	1	4	0	0	0
89	0	0	0	2	1	8	0	0	0
90	0	0	0	10	9	25	0	0	0
91	0	0	0	1	2	84	0	0	0
103	0	0	4	0	0	1	0	0	0
104	0	0	0	1	3	9	0	0	0
105	1	1	2	1	5	17	0	0	0
106	0	0	0	0	2	8	0	0	0
107	0	1	3	12	4	24	0	0	0
108	0	0	0	2	2	38	0	0	0
109	1	0	1	0	0	4	0	0	0
110	0	0	5	3	0	4	0	0	0
111	0	0	0	5	7	35	0	0	0
112	0	0	1	1	3	7	0	0	0
113	0	0	0	2	7	56	0	0	0
114	0	0	0	11	10	64	0	0	0
115	0	0	0	0	0	19	0	0	0
125	22	21	86	0	0	0	0	0	0
126	9	13	123	0	0	274	0	0	0
127	5	17	41	0	0	4	0	0	0
128	3	5	23	0	0	2	0	0	0
129	42	28	313	0	0	7	0	0	0
130	0	1	1	0	1	1	0	0	0
131	0	0	0	12	18	42	0	0	0
132	16	0	82	1	0	10	0	0	0
133	15	12	62	1	4	7	0	0	0
134	0	0	0	0	1	2	0	0	0
135	0	0	0	14	12	26	0	0	0
147	11	4	50	0	0	0	0	0	0
148	0	0	0	0	0	1	0	0	0
149	2	7	24	0	0	0	0	0	0
Total	127	110	821	95	108	829	56	61	726

for common dolphins and striped dolphins (Table 6). Kill data are also presented by year, sex and area for rough-toothed and bottlenose dolphins (Table 7), and by year and area for unidentified dolphins (Table 8). In Tables 2–7, which were derived from the tally databases, the stock or species totals may be larger than the sum over sex because the sex of some animals in the tally databases was not determined. The unidentified dolphins (Table 8) were probably spotted or spinner dolphins which were not seen closely enough for identification.

Length frequencies for sexed animals are tabulated by year and stock for spotted dolphins (Table 9), spinner dolphins (Table 10), and by year for common, striped, rough-toothed and bottlenose dolphins (Table 11). The length frequency totals (Tables 9–11) are less than or equal to the kill by sex and area totals (Tables 2–7) because lengths were obtained from the life history databases, which contain data for only a subset of the animals in the tally databases.

Perrin, Scott, Walker and Cass (1985) reviewed all body length data for specimens collected through 1981. Some of the male northern offshore spotted dolphin specimens collected after 1981 were quite large (Table 9); however, all lengths were within the range of body lengths observed by Perrin *et al.* (1985) except the 250 cm specimen recorded in 1982. The male eastern spinner dolphin in the 60–64 cm length category (Table 10) may have been an aborted fetus rather than a neonate.

Female reproductive condition results are reported by year and stock for spotted dolphins (Table 12), spinner dolphins (Table 13), and by year for common and striped dolphins (Table 14). From 1982 to 1984, no sexually mature specimens of rough-toothed or bottlenose dolphins, or of short-finned pilot whales were collected. Finally, the geographical distribution of kills is presented in Figs 1–3.

(*Text continues on page 374*)

Table 4

Total kill of spinner dolphins by observed US vessels during 1983, by stock, sex (M = male, F = female), and 5 degree block number. Reported kill of one unidentified spinner dolphin is not included. No kills were reported for the Costa Rican stock

5°	Eastern			Northern whitebelly			Southern whitebelly		
block	M	F	Total	M	F	Total	M	F	Total
23	0	0	0	0	0	0	0	2	4
24	0	0	0	0	0	0	1	0	12
25	0	0	0	0	0	0	11	11	99
26	0	0	0	0	0	0	1	1	3
44	0	0	0	0	0	0	11	19	59
45	0	0	0	0	0	0	5	3	17
46	0	0	0	0	0	0	1	4	7
64	0	0	0	0	0	0	7	6	36
65	0	0	0	0	0	0	1	3	6
66	0	0	0	0	0	0	6	6	32
67	0	0	0	0	0	0	1	0	2
86	0	0	0	0	1	3	0	0	0
88	0	0	0	0	0	1	0	0	0
90	0	1	1	0	0	0	0	0	0
105	1	0	2	0	0	0	0	0	0
107	0	0	0	0	0	3	0	0	0
110	0	0	2	0	0	1	0	0	0
111	0	0	0	0	0	1	0	0	0
112	0	0	0	2	0	2	0	0	0
114	0	0	0	1	0	1	0	0	0
115	0	0	0	1	1	2	0	0	0
126	0	0	55	0	0	0	0	0	0
128	2	4	40	6	8	14	0	0	0
129	10	9	28	0	0	0	0	0	0
130	4	3	14	0	1	3	0	0	0
131	8	9	61	3	0	10	0	0	0
132	0	0	0	15	21	445	0	0	0
133	0	1	4	35	53	400	0	0	0
135	0	0	0	10	5	23	0	0	0
148	2	2	7	0	0	0	0	0	0
149	1	1	2	0	0	1	0	0	0
151	0	0	0	3	2	26	0	0	0
Total	28	30	216	76	92	936	45	55	277

Table 5

Total kill of spinner dolphins by observed US vessels during 1984, by stock, sex (M = male, F = female), and 5 degree block number. Reported kill of 176 unidentified spinner dolphins is not included. No kills were reported for the Costa Rican stock

5°	Eastern			Northern whitebelly			Southern whitebelly		
block	M	F	Total	M	F	Total	M	F	Total
23	0	0	0	0	0	0	0	0	2
24	0	0	0	0	0	0	26	26	74
44	0	0	0	0	0	0	9	2	13
45	0	0	0	0	0	0	0	1	16
65	0	0	0	0	0	0	0	0	4
85	0	0	0	1	0	38	0	0	0
86	0	0	0	0	1	1	0	0	0
87	0	0	0	4	5	122	0	0	0
88	0	0	0	3	1	8	0	0	0
89	0	0	0	0	0	3	0	0	0
106	0	0	0	0	1	1	0	0	0
107	0	0	0	25	15	56	0	0	0
108	4	5	9	6	5	51	0	0	0
110	0	0	0	33	29	62	0	0	0
111	0	0	0	9	13	36	0	0	0
112	0	0	0	5	7	30	0	0	0
113	0	0	0	1	3	4	0	0	0
114	0	0	0	4	12	25	0	0	0
125	43	14	442	0	0	0	0	0	0
126	1	2	3	0	0	0	0	0	0
127	2	3	6	1	3	6	0	0	0
128	43	32	193	33	22	55	0	0	0
129	1	0	2	0	1	1	0	0	0
131	7	9	37	1	2	6	0	0	0
132	1	0	1	6	4	14	0	0	0
133	0	0	1	0	0	0	0	0	0
134	0	0	0	0	0	96	0	0	0
148	2	0	8	0	0	5	0	0	0
Total	104	65	702	132	124	615	35	29	109

Table 6

Total kill of common and striped dolphins by observed US vessels, by year, sex (M = male, F = female), and 5 degree block number. T = total

	1982						1983						1984					
5°	Common			Striped			Common			Striped			Common			Striped		
block	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T
24	0	0	0	4	1	179	0	0	0	0	0	1	1	0	1	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
45	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
104	1	5	7	0	0	0	3	4	19	0	0	0	0	0	0	0	0	0
105	11	29	128	0	0	0	1	5	14	0	0	0	0	0	0	0	0	0
106	2	7	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	1	2	10	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	3	2	8	0	0	0	4	7	743	4	5	9
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
148	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
149	2	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
169	0	0	0	0	0	0	9	16	25	0	0	0	0	0	0	0	0	0
170	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
189	0	0	71	0	0	0	18	13	33	0	0	0	0	0	0	0	0	0
Total	16	43	227	5	3	190	34	40	99	0	0	1	5	7	744	4	5	10

Table 7

Total kill of rough-toothed and bottlenose dolphins by observed US vessels, by year, sex (M = male, F = female), and 5 degree block number. Reported kills of 36 rough-toothed dolphins (2 males, 6 females, 28 sex undetermined) at an unknown position and of 2 short-finned pilot whales of undetermined sex during 1982 are not included. No kills were reported for rough-toothed or bottlenose dolphins, or for short-finned pilot whales during 1984

	1982						1983					
5°	Rough-toothed			Bottlenose			Rough-toothed			Bottlenose		
block	M	F	Total	M	F	Total	M	F	Total	M	F	Total
105	0	0	0	0	0	0	0	0	0	1	0	1
107	0	0	0	1	0	1	0	0	0	0	0	0
111	0	0	1	0	0	0	0	0	0	0	0	0
125	0	1	1	0	0	1	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	2	0	2
128	0	0	0	0	1	2	0	0	0	0	0	0
130	0	0	0	0	0	0	0	1	1	0	0	0
170	0	0	0	0	0	1	0	0	0	0	0	0
Total	0	1	2	1	1	5	0	1	1	3	0	3

Table 8

Total kill of unidentified dolphins by observed US vessels, by year and 5 degree block number. Sex was not determined for these animals

5° block	1982	1983	1984	5° block	1982	1983	1984
24	0	0	4	112	4	1	0
45	3	0	0	113	5	0	0
64	15	0	0	126	1	0	0
66	10	0	0	127	1	0	0
67	0	1	0	128	3	3	5
68	1	0	0	129	43	0	0
83	10	0	0	130	0	1	0
85	3	0	0	132	24	15	0
91	51	0	0	133	23	3	0
92	1	0	0	147	5	0	0
105	2	0	0	148	0	8	1
106	12	0	0	151	0	4	0
111	2	0	2	Total	219	36	12

Table 9

Length frequencies of spotted dolphins killed by observed US vessels, by year, stock, and sex (M = male, F = female). Reported kill during 1983 of one 214–219 cm male belonging to the coastal stock is not included. No kills were reported for the coastal stock during 1982 and 1984

Length (cm)	1982				1983				1984			
	Northern offshore		Southern offshore		Northern offshore		Southern offshore		Northern offshore		Southern offshore	
	M	F	M	F	M	F	M	F	M	F	M	F
0–74	0	0	0	0	0	0	0	0	0	0	0	0
75–79	1	0	0	0	0	0	0	0	0	0	0	0
80–84	3	4	0	0	0	0	0	0	0	1	1	2
85–89	4	1	0	0	2	0	1	2	2	1	4	5
90–94	2	5	0	0	0	0	1	1	4	6	2	1
95–99	2	4	0	1	0	0	1	1	1	1	0	0
100–104	2	6	0	0	0	2	0	0	1	4	0	0
105–109	3	3	0	0	0	0	0	1	3	0	0	0
110–114	2	2	0	0	0	1	0	0	4	1	0	0
115–119	8	7	3	0	0	1	0	0	1	1	0	0
120–124	7	15	1	1	2	1	1	1	3	3	0	0
125–129	5	6	3	1	1	1	0	0	1	1	0	0
130–134	5	7	0	1	0	1	1	0	3	2	0	1
135–139	5	6	1	1	1	1	1	0	4	7	2	0
140–144	9	6	1	1	1	0	0	0	6	6	0	0
145–149	6	13	4	1	3	2	0	3	6	12	0	0
150–154	19	14	3	2	4	5	3	2	9	9	1	0
155–159	21	16	11	5	8	6	1	0	16	13	0	0
160–164	18	28	7	10	8	12	2	11	18	17	2	1
165–169	24	29	10	11	9	13	4	4	14	22	5	3
170–174	32	32	9	16	9	7	9	3	25	27	4	3
175–179	31	38	9	21	10	12	4	10	20	44	2	4
180–184	23	66	5	32	10	7	4	15	17	47	4	7
185–189	29	86	11	37	5	23	5	17	29	63	1	4
190–194	28	85	9	33	17	22	5	22	29	49	1	7
195–199	47	59	12	13	8	18	6	9	31	36	3	6
200–204	43	26	9	2	6	2	10	4	17	18	1	1
205–209	33	10	5	1	4	0	6	0	20	4	1	0
210–214	19	4	4	0	6	0	2	0	9	3	1	0
215–219	8	0	3	0	2	0	1	0	6	1	1	0
220–224	7	0	0	0	0	0	0	0	2	0	0	0
225–229	1	0	0	0	0	0	0	0	0	0	0	0
230–234	0	0	0	0	0	0	0	0	1	0	0	0
235–249	0	0	0	0	0	0	0	0	0	0	0	0
250–254	1	0	0	0	0	0	0	0	0	0	0	0
255–	0	0	0	0	0	0	0	0	0	0	0	0
Total	448	578	120	190	116	137	68	106	302	399	36	45

Table 10

Length frequencies of spinner dolphins killed by observed US vessels, by year, stock (E = eastern, NWB = northern whitebelly, SWB = southern whitebelly) and sex (M = male, F = female). Reported kills of 12 unidentified spinners during 1982, 1 unidentified spinner during 1983, and 70 unidentified spinners during 1984 are not included. No kills were reported for the Costa Rican stock during 1982–84

Length (cm)	1982						1983						1984					
	E		NWB		SWB		E		NWB		SWB		E		NWB		SWB	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
0–59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60–64	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
65–74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75–79	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0
80–84	0	0	0	1	0	0	0	0	2	2	0	0	0	0	0	0	0	0
85–89	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
90–94	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
95–99	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	2	0	0
100–104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
105–109	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
110–114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
115–119	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
120–124	0	3	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0
125–129	0	1	0	3	1	0	1	0	2	0	0	0	0	0	0	1	0	0
130–134	0	0	3	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0
135–139	1	1	1	0	1	1	1	0	0	1	0	0	0	1	1	0	0	0
140–144	1	0	1	4	0	0	0	1	0	1	0	0	0	4	4	0	0	0
145–149	2	3	3	2	0	1	0	3	4	2	1	0	0	1	1	0	0	0
150–154	5	4	2	2	0	3	1	1	2	4	2	2	1	1	5	6	1	0
155–159	3	5	6	9	1	2	2	2	6	3	0	0	2	6	5	3	0	0
160–164	8	8	5	11	2	3	4	3	5	5	1	2	4	2	10	8	4	3
165–169	9	15	9	6	4	7	2	3	4	8	2	2	4	7	11	15	3	0
170–174	8	15	8	14	3	9	1	2	5	13	0	3	7	4	11	12	3	2
175–179	11	4	4	16	15	9	3	4	8	17	2	11	7	3	7	15	2	5
180–184	5	5	10	8	13	10	4	2	8	10	5	15	2	1	9	11	7	8
185–189	2	1	11	8	11	9	0	0	6	6	15	8	4	2	6	5	7	3
190–194	0	0	5	7	11	2	0	0	2	0	6	3	4	1	2	5	6	6
195–199	0	0	6	0	5	2	0	0	0	0	2	1	0	0	1	0	1	0
200–204	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	1
205–209	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
210–214	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
215–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	58	67	77	96	70	60	19	23	55	72	38	47	39	36	78	87	35	29

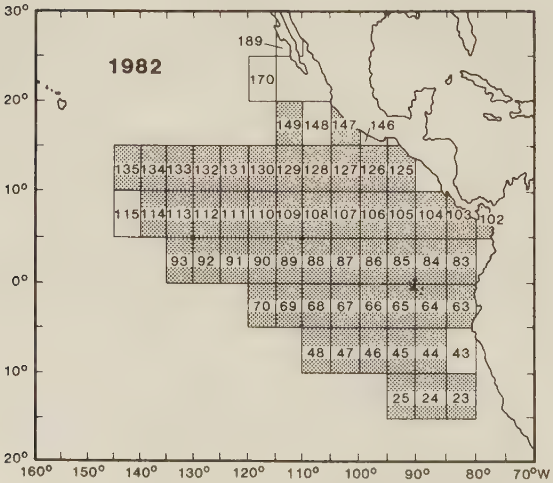
1982
189
170
149 148 147 146
135 134 133 132 131 130 129 128 127 126 125
115 114 113 112 111 110 109 108 107 106 105 104 103 102
93 92 91 90 89 88 87 86 85 84 83
70 69 68 67 66 65 64 63
48 47 46 45 44 43
25 24 23
30°
20°
10°
0°
10°
20°
160° 150° 140° 130° 120° 110° 100° 90° 80° 70°W

Fig 1. Five-degree blocks in the eastern tropical Pacific Ocean in which dolphins were killed during fishing operations of US vessels in 1982. Numbered blocks without shading indicate areas in which tally data only were collected. Numbered blocks with shading indicate areas in which no dolphin kills were recorded.

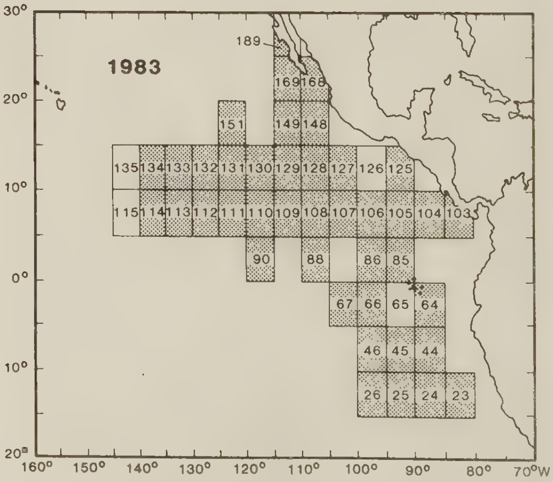
1983
189
169 168
151
149 148
135 134 133 132 131 130 129 128 127 126 125
115 114 113 112 111 110 109 108 107 106 105 104 103
90 88 86 85
67 66 65 64
46 45 44
26 25 24 23
30°
20°
10°
0°
10°
20°
160° 150° 140° 130° 120° 110° 100° 90° 80° 70°W

Fig. 2. Five-degree blocks in the eastern tropical Pacific Ocean in which dolphins were killed during fishing operations of US vessels in 1983, with block numbering and shading conventions as in Fig. 1.

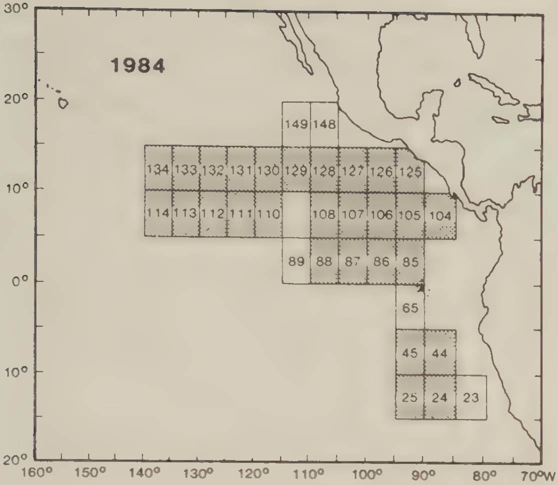

Fig. 3. Five-degree blocks in the eastern tropical Pacific Ocean in which dolphins were killed during fishing operations of US vessels in 1984, with block numbering and shading conventions as in Fig. 1.

Table 11

Length frequencies of common, striped, rough-toothed, and bottlenose dolphins killed by observed US vessels, by year and sex (M = male, F = female). Reported kills of 1 female bottlenose dolphin (220–224 cm) during 1982 and 1 female rough-toothed dolphin (210–214 cm) during 1983 are not included. No kills were reported of striped dolphins during 1983, and no kills were reported of rough-toothed or bottlenose dolphins during 1984

	1982						1983				1984			
Length (cm)	Common		Striped		Rough-Toothed		Common		Bottlenose		Common		Striped	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F
0–89	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90–94	0	1	0	0	0	0	1	0	0	0	0	0	0	0
95–99	1	0	0	0	0	0	0	0	0	0	0	0	0	0
100–119	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120–124	0	0	0	0	0	0	0	0	0	0	0	0	0	1
125–129	0	0	0	0	0	1	0	0	0	0	0	0	0	0
130–134	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135–139	0	1	0	0	0	0	0	0	0	0	0	0	1	0
140–144	1	0	0	0	0	0	0	0	0	0	0	0	0	0
145–149	1	0	0	0	0	0	1	1	0	0	0	0	0	0
150–154	0	0	0	0	0	0	0	1	0	0	0	0	1	0
155–159	1	1	0	0	0	0	0	0	0	0	0	0	0	0
160–164	0	2	0	0	0	0	0	1	0	0	0	0	0	0
165–169	0	1	1	0	0	0	0	1	0	0	0	0	0	1
170–174	0	0	0	1	0	1	1	3	0	0	0	0	0	0
175–179	1	1	0	0	0	0	2	0	0	0	0	0	0	1
180–184	0	3	0	0	0	0	3	3	0	0	0	0	0	0
185–189	1	6	0	0	0	1	1	2	0	0	0	0	1	0
190–194	1	8	0	0	0	0	2	1	0	0	1	0	0	0
195–199	0	8	0	0	0	0	1	4	0	0	0	0	0	1
200–204	1	4	1	0	0	1	0	5	0	0	0	1	1	0
205–209	3	5	0	1	0	0	2	4	0	0	0	0	0	1
210–214	2	1	0	0	0	1	3	2	0	0	1	0	0	0
215–219	2	0	2	0	0	1	3	2	0	0	0	0	0	0
220–224	1	0	0	0	1	1	3	3	0	0	0	0	0	0
225–229	0	0	0	0	1	0	4	1	0	0	0	0	0	0
230–234	0	0	0	0	0	0	3	0	0	0	0	0	0	0
235–239	0	0	0	0	0	1	0	0	0	0	0	0	0	0
240–249	0	0	0	0	0	0	0	0	0	0	0	0	0	0
250–254	0	0	0	0	0	0	0	0	1	0	0	0	0	0
255–259	0	0	0	0	0	0	0	0	0	0	0	0	0	0
260–264	0	0	0	0	0	0	0	0	1	0	0	0	0	0
265–269	0	0	0	0	0	0	0	0	1	0	0	0	0	0
270–	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	16	42	4	2	2	8	30	34	3	0	2	1	4	5

Table 12

Reproductive condition of female spotted dolphins killed by observed US vessels, by year and stock. Both sample sizes (N) and percentages (%) are indicated. Reproductive condition information was not obtained for any animals belonging to the coastal stock. U = Maturity undetermined; I = Sexually immature; MU = Sexually mature, condition undetermined; P = Pregnant only; PL = Pregnant and lactating; L = Lactating only; RCL = 'Resting' with corpus luteum; R = 'Resting' without corpus luteum; PR = Post-reproductive

	1982				1983				1984			
	Northern offshore		Southern offshore		Northern offshore		Southern offshore		Northern offshore		Southern offshore	
	N	%	N	%	N	%	N	%	N	%	N	%
U	336	57.9	78	41.1	62	45.3	69	65.1	230	57.6	40	88.9
I	90	15.5	44	23.2	38	27.7	15	14.2	81	20.3	1	2.2
MU	0	0.0	1	0.5	0	0.0	0	0.0	1	0.3	0	0.0
P	39	6.7	15	7.9	10	7.3	4	3.8	31	7.8	2	4.4
PL	9	1.6	5	2.6	4	2.9	0	0.0	2	0.5	0	0.0
L	77	13.3	30	15.8	21	15.3	6	5.7	38	9.5	1	2.2
RCL	4	0.7	3	1.6	0	0.0	2	1.9	4	1.0	0	0.0
R	23	4.0	13	6.8	2	1.5	10	9.4	11	2.8	1	2.2
PR	2	0.3	1	0.5	0	0.0	0	0.0	1	0.3	0	0.0
Total	580	100.0	190	100.0	137	100.0	106	100.0	399	100.0	45	100.0

Table 13

Reproductive condition of female spinner dolphins killed by observed US vessels, by year and stock. Both sample sizes (N) and percentages (%) are indicated. Reproductive condition information was not obtained for any animals belonging to the Costa Rican stock. During 1983, none of the 23 eastern spinner, 72 northern whitebelly, or 47 southern whitebelly specimens was sexually mature. Abbreviations as for Table 12

	1982						1984					
	Eastern		Northern whitebelly		Southern whitebelly		Eastern		Northern whitebelly		Southern whitebelly	
	N	%	N	%	N	%	N	%	N	%	N	%
U	45	67.2	65	71.4	56	91.8	27	45.8	63	72.4	27	93.1
I	15	22.4	17	18.7	2	3.3	21	35.6	11	12.6	0	0.0
MU	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
P	1	1.5	1	1.1	0	0.0	3	5.1	1	1.1	0	0.0
PL	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
L	6	9.0	3	3.3	2	3.3	6	10.2	9	10.3	2	6.9
RCL	0	0.0	0	0.0	1	1.6	0	0.0	1	1.1	0	0.0
R	0	0.0	5	5.5	0	0.0	2	3.4	2	2.3	0	0.0
PR	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Total	67	100.0	91	100.0	61	100.0	59	100.0	87	100.0	29	100.0

Table 14

Reproductive condition of female common and striped dolphins killed by observed US vessels, by year. Both sample sizes (N) and percentages (%) are indicated. During 1983, none of the 34 common dolphin specimens was sexually mature, and no reproductive condition information was obtained for striped dolphins. During 1984, no reproductive condition information was obtained for common dolphins

	1982				1984	
	Common		Striped		Striped	
	N	%	N	%	N	%
M	28	66.7	0	0.0	1	20.0
I	7	16.7	1	50.0	2	40.0
MU	0	0.0	0	0.0	0	0.0
P	1	2.4	1	50.0	1	20.0
PL	1	2.4	0	0.0	0	0.0
L	4	9.5	0	0.0	1	20.0
RCL	1	2.4	0	0.0	0	0.0
R	0	0.0	0	0.0	0	0.0
PR	0	0.0	0	0.0	0	0.0
Total	42	100.0	2	100.0	5	100.0

DISCUSSION

There are two differences between the data treatment here compared to that in the two previous papers in this series. Firstly, as noted above, tally data from IATTC technicians were not included in other papers. Inclusion of tally data from IATTC technicians allowed us to obtain sex breakdown for a larger proportion of animals than possible from the life history data. Secondly, results for common and striped dolphins are reported as species totals here rather than as separate subtotals for each geographic stock.

The unusually small number of common dolphins which were sexed out of the total kill of 744 in 1984 (Table 6), is correct as reported. Nearly all of these animals were killed in one haul of the purse–seine net, making it impossible to examine more than a very small fraction of the dead animals.

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86137

21. Geographical variation and biology of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, in the north-eastern Pacific

William A. Walker, Stephen Leatherwood,
Kimberley R. Goodrich, William F. Perrin, and
Richard K. Stroud

INTRODUCTION

The Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, is a North Pacific endemic reported from Taiwan to the Kurile and Commander Islands on the west (Okada and Hanaoka 1939; Sleptsov 1961; Nishiwaki 1967; Tomilin 1967; Mitchell 1975), from 20° 21°N to 61°N on the east, and more-or-less continuously across temperate waters between 40° and 46°N (Leatherwood and Walker 1982, Leatherwood, Reeves, Bowles, Stewart, and Goodrich 1984). The species was described by Gill (1865) based on three co-types (U.S. National Museum Nos. 1961, 1962, 1963) reportedly taken 'off the California coast.' Though the exact locality is unclear, Poole and Shantz (1942) list the type specimen (three skulls with mandibles, in good condition) as having been taken by W. P. Trowbridge from near San Francisco, San Mateo County and catalogued 14 October 1885. They attribute these details to True (1889). A careful reading of the latter indicates that the specimens were indeed obtained 'on the coast of California by Lieutenant W. P. Trowbridge' but that for the types and for another specimen (USNM 14329) discussed in the same paragraph '. . . no particular localities are given in either instance.'

The species *Lagenorhynchus ognevi* Sleptsov (1955) was also described from the North Pacific, but it is now thought to be invalid. Tomilin (1967) demonstrated that the diagnostic characters based on cranial and postcranial morphology and meristics as well as external morphology and colouration are largely age-related features and well within the limits of variation found in *L. obliquidens*.

In the north-eastern Pacific, white-sided dolphins are widely distributed, at least seasonally, between about 23°N and the northern Gulf of Alaska and northern North Pacific. Within that range, seasonal fluctuations in apparent abundance, thought to be related to shifts in population centre(s), are reported for northern California, the Southern California Bight, and the west coast of Baja California (Leatherwood and Walker 1982; Leatherwood *et al.* 1984).

In 1979 we began a study on geographical variation and biology of *L. obliquidens* in the eastern North Pacific. The primary objectives were to investigate the possible existence of subpopulations in the study area and to increase our knowledge of the general biology of the species.

METHODS

External measurements, ranging from total length only to a complete set of measurements, were available for 243 specimens.

Of all standard measurements taken for odontocetes, total length is that most likely to be taken consistently. Even so, length measurements were screened carefully before being used in any further analysis. We consider that all other measurements are less likely to be consistently reliable. They were taken over a long period (1905–1982) by a variety of workers using various and often unreported techniques. Therefore, we did not attempt to use such measurements in any analyses to differentiate populations.

Cranial measurements were selected and taken following Perrin (1975) (Table 1). As in previous studies of this kind, juvenile specimens were excluded from consideration because of ontogenetic growth changes and their effect on the analysis of population differences. Because rostral distal fusion, a feature used to indicate the onset of sexual maturity in *Stenella* spp. (Dailey and Perrin 1973) and *Tursiops* sp. (Walker 1981), does not occur in even physically mature specimens of *Lagenorhynchus obliquidens*, we determined state of maturity using other criteria:

(1) reproductive condition, judged by direct analysis of organs or availability of other data indicating sexual maturity, such as notes on lactation or presence of a foetus;
(2) evidence of fusion in thoracic vertebral epiphyses;
(3) presence of seven or more growth layer groups in teeth; or
(4) in the absence of other data, evidence from the overall development of cranial sutures that the animal was at least sexually mature.

One hundred and fifty-two crania (73 females, 60 males, and 19 animals of undetermined sex) from the north-eastern Pacific, between about 24°30′N and 61°N, were measured. One hundred and twelve of these (74%) were from the area of southern California between 32° and 37°N, 31 (20%) were from north of 37°N, and nine (6%) were from below 32°N. The gaps between the localities of the sample from southern California and those from the extreme northern and extreme southern portions of the eastern Pacific range were useful in grouping skulls for analysis.

In multivariate analyses, specimens with missing measurements are eliminated from the sample. To counter this problem and to maintain the highest possible sample size, we eliminated those measurements which are commonly missing due to damage during collection and preparation of specimens (see Table 21.1).

Teeth were collected from near the middle of the left lower jaw of 142 animals (86 females, 56 males) for which total length and collection location were known. The teeth were prepared at NMFS/SWFC following procedures detailed by Myrick, Hohn, Sloan, Kimura, and Stanley (1983). Decalcification times ranged from 11.5 to 20.0 h, increasing with tooth and pulp cavity size. Staining times ranged from 30 to 60 minutes.

Dentinal growth layer groups (GLGs; terminology of Perrin and Myrick 1981) of *L. obliquidens* are composed of four alternating lightly and darkly stained bands. The first band or boundary layer (beginning with the neonatal line) is thin and either unstained or lightly stained. Within the GLG and advancing toward the pulp cavity this band is adjacent to first a broad darkly stained band, then a thin unstained mid-GLG band, and finally a broad dark band. Cemental GLGs are composed of two bands, one darkly and one lightly stained.

Each tooth section was independently read twice by each of two readers (Goodrich and Myrick). Following a cursory examination of the condition of the section, dentinal readings were made. Counts of dentinal layers were supplemented by counts of cemental layers, recognizing that the latter often occur in multiples of the former. Whenever the pulp cavity was occluded or dentinal layers were poorly stained, cemental layers were considered the most reliable indicators of GLGs.

'Best' and 'final' counts, considering size of the pulp cavity and condition of GLG layers (see protocol, Myrick *et al.* 1983), were averaged. If any 'best and final' readings were outside a pre-established interval from that mean (± 1 for 0–10 GLGs, ± 2 for 11–15 GLGs, ± 3 for 16–25 GLGs, ± 4 for 26–36 GLGs, and ± 5 for ⩾37 GLGs) the tooth was reread. Results of all readings ('best' initial and reread values) were used to calculate mean GLGs for each specimen. The data are summarized in Walker, Goodrich, Leatherwood, and Stroud (1984).

Previously unpublished reproductive data from 88 specimens (50 females and 38 males) are presented (Tables 21.2 and 21.3). Laboratory procedures for preparation and examination of reproductive tissue samples followed Perrin, Coe, and Zweifel (1976).

As in previous studies, sexual maturity in the present sample was judged from presence of at least one corpus luteum or corpus albicans or presence of sperm in a testis section, supplemented by other data available, such as testis weight, lactation, or evidence of pregnancy.

Information on colour pattern in *L. obliquidens* was derived from examination of numerous photographs and the authors' (Walker and Leatherwood) personal observations of free-ranging and captive animals.

Stomach contents of 23 animals were available for analysis. All were from

TABLE 21.1. *Skull measurements (in mm) and meristics of* Lagenorhynchus obliquidens *from the north-eastern Pacific*

Variable		Sample	Range (mm)	Mean	Stand. Dev.
* 1	Condylobasal length	144	350–446	388.0	16.2
* 2	Rostrum length	144	171–228	195.6	10.3
* 3	Rostrum width at base	146	91–123	105.6	6.6
* 4	Rostrum width at 60 mm	145	66–95	78.6	6.2
* 5	Rostrum width at midlength	142	60–86	70.9	5.5
* 6	Premaxillary width at rostrum midlength	144	36–56	43.8	3.9
* 7	Rostrum width at $\frac{3}{4}$ length	142	43–70	54.6	5.2
* 8	Rostrum tip to external nares	144	208–273	237.9	11.3
* 9	Rostrum tip to internal nares	123	206–277	243.8	12.9
*10	Preorbital width	139	164–198	178.0	7.6
*11	Postorbital width	141	181–214	194.5	7.2
*13	External nares width	146	44–90	56.9	4.8
*14	Zygomatic width	144	178–218	195.1	8.3
*15	Greatest width of premaxillaries	147	80–103	89.9	3.6
*16	Parietal width	144	148–184	168.8	6.2
*19	Temporal fossa length	147	65–93	79.7	5.8
*20	Temporal fossa width	148	50–78	60.8	4.9
*25	Orbit length	141	47–65	53.9	3.0
*26	Antorbital process length	142	25–47	36.1	3.6
*27	Internal nares width	144	48–75	61.7	4.7
28	Pterygoid length	142	53–74	62.8	4.6
30	Bulla length	89	29–38	35.2	1.6
31	Periotic length	81	28–37	30.5	1.4
32	Upper tooth row length	142	154–213	179.1	9.9
33–36	Teeth (no.)	140/138	24–36/25–35	30.3/30.5	2.1/2.2
		145/144	23–34/25–35	30.1/30.1	2.0/2.0
37	Lower tooth row length	140	165–214	180.6	9.0
38	Ramus length	137	231–366	320.2	15.6
39	Ramus height	139	60–81	68.6	3.9
40	Tooth width	127	3.2–6.5	4.6	0.5

*Indicates measurements in principal components analyses.

Note: Data from both populations are pooled. These calculations are presented solely to characterize cranial features of *Lagenorhynchus obliquidens* and to facilitate comparisons with other species of *Lagenorhynchus*.

TABLE 21.2. *Summary of female reproductive data for* Lagenorhynchus obliquidens *from the north-eastern Pacific*

Specimen No.	Location Lat (N)	Location Long (W)	Collection Date YMD	Mean GLG No.	Weight (kg)	Total Length (cm)	Gonad Weights Left	Gonad Weights Right	No. of Corpora Left	No. of Corpora Right	Source of Data or Reproductive Specimens	Reproductive Comments
NMML 3223	37°42′	123°08′	66-03-25	7.8	65	159	3.3	2.7	0	0	NMML	Follicle diameter: 35–40 microns
L-02-19	34°07′	119°06′	67-07-13	—	—	162	5.5	5.5	—	—	NUC	——
NMML 3208	35°04′	121°33′	66-03-09	4.0	66	162	1.2	1.2	0	0	NMML	Immature, follicle diameter; 0.5 mm
NMML 3277	46°14′	124°40′	68-02-26	6.8	67	165	1.3	1.1	0	0	NMML	Immature, follicle diameter: 0.9 mm
NMML 3273	46°14′	124°40′	68-02-26	—	71	167	2.2	3.1	0	0	NMML	Follicle diameter: left 1.7 mm; right 2.9 mm
NMML 3790	36°25′	122°31′	65-06-19	7.2	73	168	6.3	3.8	0	0	NMML	Follicle diameter: left 6.7 mm; right 3.1 mm
18-68	33°30′	118°25′	68-02-28	—	—	168	1.0	0.9	0	0	Harrison *et al.* (1972)	No follicles over 100 microns
NMML 3765	37°46′	123°26′	66-02-25	9.8	73	168	4.8	2.3	0	0	NMML	Follicle diameter: left 5.1 mm; right 1.9 mm
06-63	33°45′	118°25′	63-05-04	—	68	169	—	—	0	0	Harrison *et al.* (1972)	Few small follicles 350 microns in both ovaries
TAC-59-3	35°42′	121°41′	59-02-27	—	85	170	—	—	0	0	Fisucs and Niggol (1965)	Barely visible follicles on left ovary
NMML 3212	36°29	122°30′	66-03-05	6.8	69	171	3.0	2.6	0	0	NMML	Follicle diameter: left 2.4 mm; right 2.6 mm
HSU 2418	41°03′	124°09′	58-09-11	8.7	62	171	—	—	0	0	Houck (1961)	Follicles well developed, no corpora present
NMML 3221	37°37′	123°07′	66-03-25	24.5	83	172	4.0	2.0	17	6	NMML	Follicle diameter: left 1.6 mm; right 2.0 mm
NMML 3761	37°46′	123°26′	66-02-25	5.4	75	172	0.7	1.4	0	0	NMML	Follicle diameter: left 1.6 mm; right 4.3 mm
L-02-12	33°50′	119°10′	64-06-02	—	80	173	—	—	0	0	NUC	Lab report indicates no corpora present
38-63	33°45′	118°25′	63-10-20	—	81	173	—	7.5	—	4	Harrison *et al.* (1972)	Few follicles up to 500 microns in diameter
NMML 3209	36°29′	122°30′	66-03-05	7.0	78	173	3.8	3.2	0	0	NMML	Follicle diameter: left 1.7 mm; right 1.1 mm

TABLE 21.2. *contd.*

Specimen No.	Location Lat (N)	Location Long (W)	Collection Date YMD	Mean GLG No.	Weight (kg)	Total Length (cm)	Gonad Weights Left	Gonad Weights Right	No. of Corpora Left	No. of Corpora Right	Source of Data or Reproductive Specimens	Reproductive Comments
NMML 3222	37°40′	123°08′	66-03-25	8.5	72	173	3.1	2.3	0	0	NMML	Follicle diameter: left 2.7 mm; right 2.5 mm
NMML 3762	37°46′	123°26′	66-02-25	5.6	75	173	1.8	1.6	0	0	NMML	Follicle diameter: left 1.4 mm; right 1.7 mm
NMML 3218	35°08′	121°25′	66-03-10	5.5	83	174	5.5	2.4	1	0	NMML	Follicle diameter: left 4.0 mm; right 1.8 mm
SJSU C-195	36°48′	121°47′	77-05-04	—	—	174	—	—	—	—	SJSU	Pregnant, 84 cm fetus
NMML 3768	37°46′	123°26′	66-02-25	6.8	77	174	5.0	4.3	0	0	NMML	Follicle diameter: left 3.7 mm; right 1.9 mm
NMML 3269	46°14′	124°34′	68-02-25	—	75	174	2.6	1.8	0	0	NMML	Follicle diameter: left 4.1 mm; right 2.9 mm
TAC 21143	46°14′	124°40′	68-02-25	6.5	75	174	1.3	1.1	0	0	NMML	Follicle diameter: left 0.5 mm; right 0.4 mm
7-63	33°45′	118°25′	63-05-05	—	69	174	2.6	2.6	0	0	Harrison *et al.* (1972)	No follicles over 120 microns in either ovary
SBMNH 2347	35°06′	121°40′	81-05-03	25.0	—	175	7.2	7.1	—	—	SBMNH	Animal not pregnant or lactating
NMML 3271	46°14′	124°34′	68-02-25	—	84	175	6.1	2.1	6	0	NMML	Follicle diameter: left 2.6 mm; right 1.8 mm
NMML US-61-P1	51°45′	128°00′	61-01-26	—	89	175	2.2	—	0	—	NMML	Left ovary only: follicle diameter: 0.7 mm
32-66	33°53′	118°26′	66-08-15	5.6	66	175	2.0	2.5	0	0	Harrison *et al.* (1972)	No follicles over 120 microns in either ovary
NMML 3767	37°46′	123°26′	66-02-25	8.1	78	176	2.7	3.7	0	0	NMML	Follicle diameter: left 1.6 mm; right 1.7 mm
WAW 174	33°36′	118°09′	71-09-21	—	—	176	10.6	2.0	9	0	Swayer and Walker (1977)	——
NMML 3207	37°20′	123°38′	66-03-03	8.2	83	177	3.1	4.4	0	0	NMML	Follicle diameter: left 1.8 mm; right 3.2 mm
NMML 3270	46°14′	124°34′	68-02-25	20.0	86	177	7.8	4.1	15	0	NMML	Lactating; follicle diameter: left 1.3 mm; right 1.8 mm
NMML 3760	37°46′	123°26′	66-02-25	5.9	76	178	2.2	2.7	0	0	NMML	Follicle diameter: left 1.7 mm; right 3.0 mm

NMML 3764	37°46′	123°26′	66-02-25	5.0	78	178	5.5	4.2	0	0	NMML	Follicle diameter: left 2.7 mm; right 1.9 mm
NMML 3275	46°14′	124°33′	68-02-26	9.4	82	178	4.4	2.3	1	0	NMML	Follicle diameter: left 4.8 mm; right 2.0 mm
69-7-4	33°30′	118°25′	69-02-01	—	—	178	7.3	4.2	5	0	Harrison *et al.* (1972)	Follicle diameter: right ovary 2.0 mm
NMML 3210	36°29′	122°30′	66-03-05	8.0	89	179	3.0	6.3	0	4	NMML	Follicle diameter: left 2.3 mm; right 3.8 mm
VBS 1263	48°30′	124°20′	36-09-17	—	—	180	—	—	—	—	Scheffer and Slipp (1948)	Pregnant, 12.9 mm fetus [probably 12.9 cm]
NMML 1965-175	32°37′	118°56′	65-07-12	8.7	97	180		—	—	—	NMML	Animal pregnant, 45 cm fetus; not lactating
26-67	33°46′	118°10′	67-08-21	14.2	55	180	6.5	3.0	9	0	Harrison *et al.* (1972)	No follicles over 120 microns
NMML 3217	35°08′	121°25′	66-03-10	9.0	81	181	5.5	3.2	2	0	NMML	Follicle diameter: left 2.9 mm; right 2.5 mm
MVZ 140845	38°05′	122°55′	70-02-09	37.2	—	181	—	—	—	—	MVZ	Field records report numerous corpora albicantia on both ovaries
MLP 70-19-1	33°45′	118°25′	70-09-22	—	—	182	—	—	—	—	MLP	Captive animal; gave birth to 95 cm, 25 lb male calf; calf lived ½ hr
TAC 59-4	36°58′	122°53′	59-03-05	—	88	182	—	—	—	—	Fiscus and Niggol (1959)	"numerous follicles"; animal considered nulliparous
USNM 276395	37°45′	122°50′	48-12-12	—	—	183	—	—	—	—	Scheffer (1950)	Pregnant, 37 cm fetus
69-6-2	33°35′	118°25′	69-06-01	—	84	183	10.1	5.1	5	0	Harrison *et al.* (1972)	Animal aborted a near term fetus on 69-03-01
TAC 59-1	35°16′	121°35′	59-02-14	—	84	183	—	—	—	—	Fiscus and Niggol (1965)	Numerous follicles; apparently nulliparous
2-63	33°30′	118°35′	62-10-00	—	74	183	—	4.1	—	0	Harrison *et al.* (1972)	No follicles over 120 microns in right ovary
USNM 276395	37°45′	123°10′	48-12-12	8.6	95	183	—	—	—	—	USNM	Pregnant animal. Ranged from 3–15 mm
16-62	33°30′	118°25′	62-10-00	—	77	185	4.2	4.1	0	0	Harrison *et al.* (1972)	No follicles over 120 microns
13-62	33°57′	118°25′	62-08-24	—	65	185	8.3	13.3	0	4	Harrison *et al.* (1972)	Numerous cystic follicles from 1–2 cm diameter
LACM 54712	33°45′	118°20′	70-10-26	21.5	86	185	—	—	11	—	LACM	Necropsy records reported 11 CA's on left ovary
NMML 1968-103	33°48′	119°43′	68-02-08	19.5	88	186	—	—	—	—	NMML	Necropsy records report "many CA's" on left ovary

Table 21.2. *contd.*

Specimen No.	Location Lat (N)	Location Long (W)	Collection Date YMD	Mean GLG No.	Weight (kg)	Total Length (cm)	Gonad Weights Left	Gonad Weights Right	No. of Corpora Left	No. of Corpora Right	Source of Data or Reproductive Specimens	Reproductive Comments
NMML 985	34°07′	120°46′	64-01-08	14.2	91	186	6.8	1.9	4	0	NMML	Not lactating; mammary thickness 10 mm
SJSU 2158	36°37′	121°54′	78-04-04	—	85	186	7.4	5.6	23	12	SJSU	Follicle diameter: left 2.2 mm; right 4.3 mm
15-62	33°30′	118°25′	62-10-00	—	76	186	4.4	6.1	—	—	Harrison *et al.* (1972)	No follicles over 120 microns in either ovary
"DEBBIE"	33°30′	118°25′	69-07-05	—	—	186	3.2	2.6	—	—	Harrison *et al.* (1972)	No follicles over 120 microns in either ovary
83-66	34°25′	118°30′	66-11-30	—	66	187	14.0	5.0	18	0	Harrison *et al.* (1972)	Aborted fetus two weeks prior to death
NMML 3219	36°02′	121°58′	66-03-22	9.8	93	188	5.5	2.5	3	0	NMML	Follicle diameter: left 3.1 mm; right 2.5 mm
HSU 2689	41°35′	124°06′	78-06-08	—	80	188	5.6	—	23	—	HSU	Lactating; left ovary follicle diameter: 3.1 mm
L-13-64	34°20′	119°25′	65-05-17	—	76	190	9.0	4.0	—	—	NUC	
NMML 3216	35°08′	121°25′	66-03-10	7.2	101	191	16.8	3.0	1	0	NMML	Pregnant, 72 cm male fetus; follicle diameter: left 2.4 mm; right 1.6 mm
RB 2118	37°24′	122°27′	73-04-14	—	—	193	—	—	—	—	Ray Bandar priv. coll.	Pregnant, records indicate "full term fetus"
USNM 504416	25°22′	112°52′	76-02-11	6.9	—	197	5.3	4.7	0	0	USNM	Immature
LACM 54711	33°20′	118°25′	70-10-20	11.8	—	197	—	—	0	9	LACM	Captive animal; aborted 29 cm fetus
WAW 150	34°00′	118°48′	72-03-04	—	—	199	8.8	4.2	7	0	Sawyer and Walker (1977)	——
INIBP-Gr6501	27°10′	114°31′	65-09-18	—	—	200	—	—	0	0	NMML	"Immature, very tiny follicles"
LACM 54076	32°48′	117°17′	70-05-07	29.2	—	201	—	—	—	—	LACM	Pregnant, 81.0 cm male fetus
WFP 591	32°52′	117°15′	79-04-16	26.4	—	208	—	—	—	—	SWFC	Lab reports about 10 CA's; lactating; uterine condition postpartum

USNM 504412	25°22′	112°52′	76-02-11	18.8	142	212	28.6	4.2	4	2	USNM	Pregnant, 52 cm fetus; follicle diameter: 2.0 ; not lactating
MWD 183	26°20′	113°43′	79-08-25	19.5	145	212	15.5	5.8	14	1	SWFC	Follicle diameter: left 2.6 mm; right 3.8 mm
MM-126	33°30′	118°25′	76-07-00	—	—	213	6.9	2.7	5	1	Harrison and McBrearty (1977)	Lived 6 years in captivity
USNM 504415	25°22′	112°52′	76-02-11	26.6	140	215	12.0	3.2	10	0	USNM	Lactating; follicle diameter: left 1.4 mm; right 1.6 mm
MM-137	33°30′	118°25′	76-08-00	—	—	216	5.5	4.3	12	2	Harrison and McBrearty (1977)	Had two stillborn calves in captivity: one 101.6 cm, the other 109.2 cm
56-68	33°30′	118°25′	68-04-12	31.2	—	236	12.5	4.5	23	0	Harrison *et al.* (1972)	Few follicles 2.0 mm diameter

Source of specimens of data: NMML = National Marine Laboratory, Seattle, Washington; NUC = Naval Undersea Center, San Diego, California; SJSU = San Jose State University, San Jose, California; SBMNH = Santa Barbara Museum of Natural History, Santa Barbara, California; MVZ = Museum of Vertebrate Zoology, Berkeley, California; MLP = Marineland of the Pacific, Rancho Palos Verdes, California; USNM = U.S. National Museum, Smithsonian Institution, Washington, D.C.; LACM = Natural History Museum of Los Angeles County, Los Angeles, California; SWFC = Southwest Fisheries Center, La Jolla, California; CPSU = California Polytechnic State University, San Luis Obispo, California; SDNHM = San Diego Natural History Museum, San Diego, California; HSU = Humboldt State University. Arcata, California.

Table 21.3. *Summary of male reproductive data for* Lagenorhynchus obliquidens *from the north-eastern Pacific*

Specimen Number	Location of Collection		Date of Collection Y/M/D	Length (cm)	Weight (kg)	Mean Number GLG's	Testis Weights (gr)		Testis Length (cm)		Tubule diameter (m)	Sperm Present		Source of Data or Specimens
	Lat (N)	Long (W)					Left	Right	Left	Right		Tubules	Epididymis	
CPSU ——	35°06′	120°38′	67-03-22	148	—	—	23.5	24.0	15.0	15.0	—	—	—	CPSU
NMML 3215	36°29′	122°30′	66-03-05	151	58	5.0	15.0	12.0	—	9.0	40	No	No	NMML
NMML 3272	46°13′	124°36′	68-02-26	152	59	—	5.1	5.2	—	7.5	40	No	No	NMML
L-01-6	34°10′	119°15′	64-01-27	152	46	—	25–35	25–35	8–10	8–10	—	—	—	Ridgway and Green (1967)
L-12-55	34°20′	119°16′	67-02-24	155	—	—	—	7.5	—	7.0	—	—	No	NUC
19-67	33°52′	118°25′	67-05-10	164	64	—	14.7	18.0	8.0	8.0	90	—	No	Harrison *et al.* (1972)
NMML 3276	46°13′	124°36′	68-02-26	165	75	7.0	13.7	13.7	—	8.6	40	No	No	NMML
29-64	33°53′	118°27′	64-10-16	170	56	—	—	-	—	—	110	—	No	Harrison *et al.* (1972)
14-24	34°02′	118°50′	64-04-21	170	74	—	305.0	340.0	21.0	22.0	160	—	No	Harrison *et al.* (1972)
NMML 3766	37°46′	124°30′	66-02-25	172	79	3.6	15.0	16.0	—	9.5	50	No	No	NMML
NMML 3214	36°29′	122°30′	66-03-05	174	82	14.2	130.0	140.0	—	19.0	—	—	—	NMML
NMML 3211	36°29′	122°30′	66-03-05	177	84	15.2	130.0	150.0	—	21.0	—	—	—	NMML
17-63	33°52′	118°23′	63-12-17	178	63	—	25.0	25.0	7.3	8.5	70	—	No	Harrison *et al.* (1972)
82-66	33°25′	119°43′	66-12-21	178	55	—	14.0	22.5	8.5	8.0	70	—	No	Harrison *et al.* (1972)
NMML 3274	46°14′	124°33′	68-02-26	179	97	—	121.0	133.3	219.0	235.0	80	Yes	—	NMML
17-62	38°17′	122°28′	62-12-17	180	61	—	21.0	22.1	50.0	90.0	70	—	No	Harrison *et al.* (1972)
NMML 3206	36°23′	122°14′	66-02-17	180	78	4.8	18.0	25.0	—	120.0	70	No	No	NMML
SBMNH 11692	34°25′	119°43′	81-05-18	181	—	25.0	345.0	—	—	—	—	—	—	SBMNH
TAC 59-2	35°28′	121°38′	59-02-22	181	90	—	—	—	—	40.0	135	—	—	NMML
28-64	33°45′	118°25′	64-09-19	183	78	—	107.0	100.0	—	—	—	—	No	Harrison *et al.* (1972)
L-2	33°30′	118°22′	64-11-27	183	76	—	17.8	17.2	8.6	8.8	70	—	No	Harrison *et al.* (1972)

NMML 3213	36°29′	122°30′	66-03-05	184	99	16.2	155.0	170.0	215.0	22.0	—	—	—	NMML
27-65	34°02′	118°29′	66-07-17	184	—	—	15.0	15.5	9.5	9.5	75		No	Harrison *et al.* (1972)
NMML 3224	37°45′	123°13′	66-03-25	186	91	10.5	175.0	165.0	225.0	230.0	110	Yes	No	NMML
WFP 082	32°52′	117°15′	71-05-16	187	77	14.0	455.0	454.0			—	—	—	SWFC
68-L-17	34°10′	119°45′	64-10-27	188	72	—	35.0	35.0	—	—	—	—	—	NUC
SDNHM 21219	32°51′	117°16′	56-01-08	194	99	25.4	150.0	150.0	30.0	30.0	75	—	No	SDNHM
JEH 1051	33°44′	118°05′	81-05-16	195	79	8.4	17.0	20.0	8.2	9.0	75	No	No	LACM
RMG 4605	25°30′	113°35′	69-04-23	198	—	—	52.0	59.0	14.0	14.0	—	—	No	Harrison *et al.* (1972)
SDNHM 21223	33°30′	118°20′	57-01-24	191	125	24.6	250.0	—	30.0	—	—	—	—	SDNHM
RMG 4-68	33°30′	118°20′	57-01-24	191	—	—	250.0	—	30.0	30.0	—	—	No	Harrison *et al.* (1972)
LACM 54714	33°35′	118°12′	70-12-09	193	90	11.2	162.0	154.0	32.0	30.0	—	—	—	LACM
04-68	33°30′	118°25′	68-02-16	194	—	—	34.5	35.0	12.0	11.5	75	—	No	Harrison *et al.* (1972)
SDNHM 981	34°22′	119°42′	75-06-16	199	133	24.5	900.0	900.0	37.0	37.5	—	—	Yes	SDNHM
CPSU M-1218	35°06′	120°38′	72-08-20	200	—	—	—	—	45.0	45.0	—	—	Yes	CPSU
R&G	34°04′	119°30′	65-08-15	200	102	—	548.0	559.0	24.0	24.5	200	—	Yes	Harrison *et al.* (1972)
10-67	33°25′	119°43′	66-11-00	201	73	10.9	104.0	106.0	19.0	17.0	100	—	No	Harrison *et al.* (1972)
104-L-20	34°30′	119°40′	67-08-02	213	100	—	540.0	510.0	35.0	35.0	—	—	No	NUC
MWD 182	26°20′	113°43′	79-08-25	219	157	18.4	—	580.0	—	—	180	Yes	No	SWFC
JEH 1042	33°40′	118°01′	81-02-16	220	124	37.4	634.0	—	30.0	—	164	Yes	No	LACM
USNM 504413	25°22′	112°52′	76-02-11	228	198	17.2	316.5	326.5	31.0	31.0	205	Yes	No	USNM

Source of specimens or data: NMML = National Marine Laboratory, Seattle, Washington; NUC = Naval Undersea Center, San Diego, California; SJSU = San Jose State University, San Jose, California; SBMNH = Santa Barbara Museum of Natural History, Santa Barbara, California; MVZ = Museum of Vertebrate Zoology, Berkeley, California; MLP = Marineland of the Pacific, Rancho Palos Verdes, California; USNM = U.S. National Museum, Smithsonian Institution, Washington, D.C.; LACM = Natural History Museum of Los Angeles County, Los Angeles, California; SWFC = Southwest Fisheries Center, La Jolla, California; CPSU = California Polytechnic State University, San Luis Obispo, California; SDNHM = San Diego Natural History Museum, San Diego, California; HSU = Humboldt State University, Arcata, California.

the Southern California Bight and off the west coast of Baja California, Mexico. Of the sample, 14 animals (61%) were collected as individual strandings. The remaining nine animals were collected at sea. Two stomachs were initially preserved in formalin, which dissolves otoliths. In these instances, fish remains were identified from intact skeletal elements. The other 21 specimens were either frozen or preserved in alcohol prior to examination.

Data on the occurrence of two air sinus parasites were recorded during the course of this study. The incidence of the genus *Nasitrema* spp. (Trematoda) was based solely on published accounts, examination of unreported museum samples, and the recent dissection of four intact animals collected off the west coast of Baja California, Mexico.

Documentation of the occurrence of the nematode *Crassicauda* sp(p). was based on dissection of 39 intact animals and examination of 197 prepared cranial specimens for evidence of *Crassicauda*-related bone lesions.

During the course of the study detailed records on post-cranial bone disease were also kept. A total of 63 skeletons was examined.

RESULTS AND CONCLUSIONS

External morphometrics

Dorsal fins in *Lagenorhynchus obliquidens* vary considerably in size, and range in shape from falcate and sharply pointed to lobate and more rounded on the tip (Kasuya 1981) (Fig. 21.1). We have observed fins of both shapes in the same herds and on both males and females in captivity. As none of the standard measurements taken on odontocetes (Norris 1961) are adequate to detect such differences in fin shape, we have no data to test the relationship of dorsal fin shape to sex, length, age, or state of maturity of specimens. We hypothesize that these differences are age related and that fins begin to become lobate with the onset of physical maturity.

The largest specimens known to us are a 250 cm male (specimen MVZ 116037, collected 23 July 1950 by Seth Benson at 28°00′N, 114°45′W) and a 236 cm female (specimen 56-68, collected by W. A. Walker 12 April 1968 at 33°33′N, 118°25′W—see Harrison, Boice, and Brownell 1969).

Cranial morphometrics

The scores of individual specimens for the first two principal component axes were plotted by latitude (Figs. 21.2 and 21.3). Geographic plots of PCA scores have been used in previous studies of animal populations (Kennedy and Schnell 1978; Menozzi, Piazza, and Cavalli-Sforzza 1978; Schnell, Douglas, and Hough 1982; Douglas, Schnell, and Hough 1984). In evaluating the results of PCA, the first principal component is generally considered to

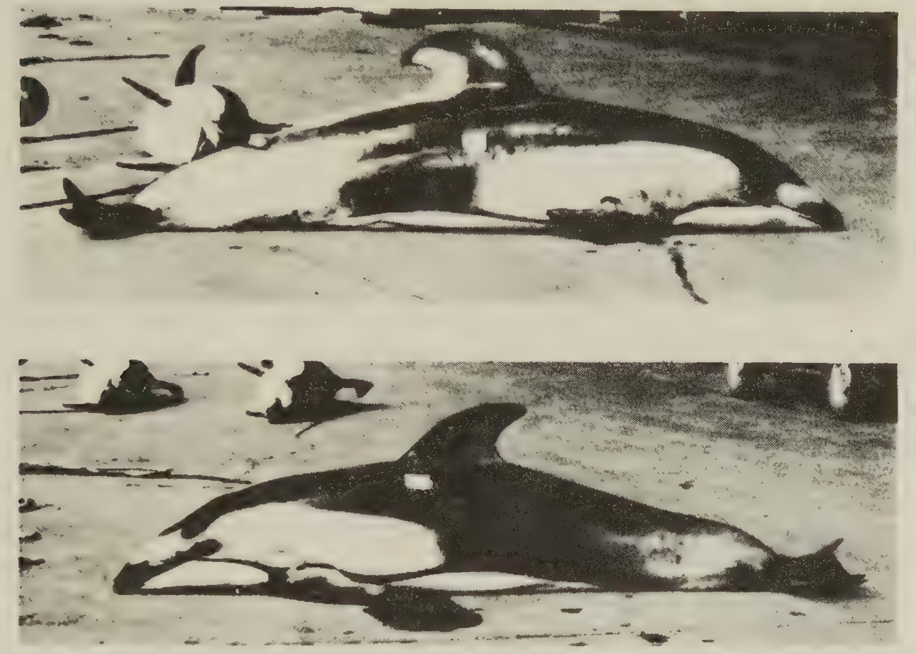

FIG. 21.1. Pacific white-sided dolphins, showing normal colouration and variability in dorsal fin size and shape (from Kasuya 1981).

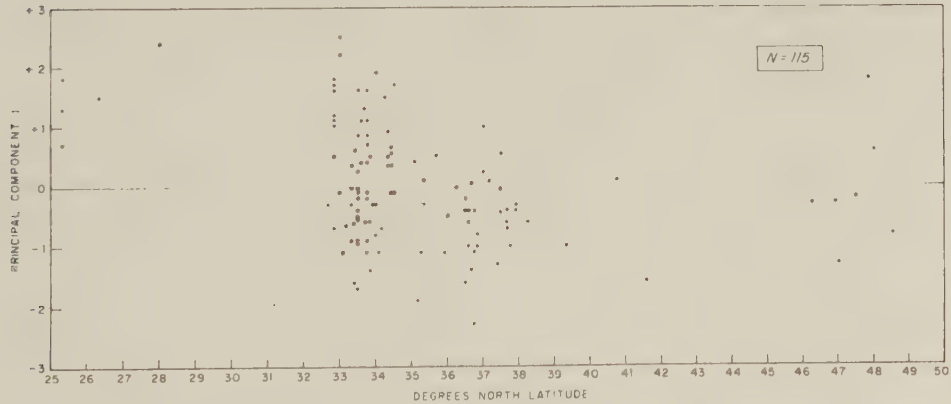

FIG. 21.2. Scores of individual cranial specimens for first principal component, by latitude.

represent specimen size, and the second to represent specimen shape (Cooley and Lohnes 1962; Seal 1964).

Though the sample in the present investigation was small, there appears to be marked separation between animals from the extreme northern (above 37°N) and southern (below 32°N) ranges of the sample with respect to size (see Fig. 21.2). The crania of southern animals tend to be larger than those of

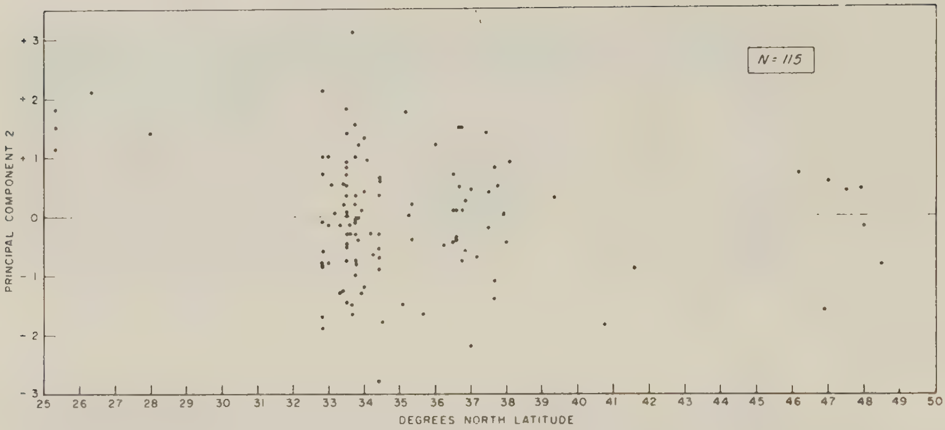

FIG. 21.3. Scores of individual cranial specimens for second principal component, by latitude.

northern animals (Fig. 21.4). We tentatively interpret these results as evidence of the existence of two populations in the north-eastern Pacific, one in the northern temperate and one in the southern temperate region. The distribution of scores for the second principal component (see Fig. 21.3) supports this interpretation, indicating that differences occur between these two putative populations in skull shape as well as skull size. It is worth noting that in both analyses there is significant variability in scores below about 37°N, with the most dramatic spread in values between 34°30′N and 32°30′N. We interpret this to possibly mean that there are specimens from both populations represented in the Southern California Bight sample. That interpretation is supported by the age–length data discussed below. The dramatic change in character of the sample latitudinally (see Figs. 21.2 and 21.3) corresponds to changes in oceanographic condition near Point Conception (approx. 34°30′N), changes which result in marked faunal differences north and south of the Point (Hubbs 1960).

The relationship between total length of the skull (CBL), and length of the temporal fossa also indicates the possible existence of two populations; the temporal fossae tend to be proportionally shorter in the southern than in the northern temperate population (Fig. 21.5).

Age relationships

No experimentally calibrated teeth were available. We have assumed that one GLG = one year. With that assumption, the animals we examined ranged in age from 0.4 to 46.0 years, with significant variability in length at any given age. Animals examined from above 37°N and below 32°N ranged from 1.5 to 37 years. A comparison of total length and skull length of the northern vs southern animals of comparable age (Figs. 21.4 and 21.6) confirm that the southern form is larger in overall size than the northern form.

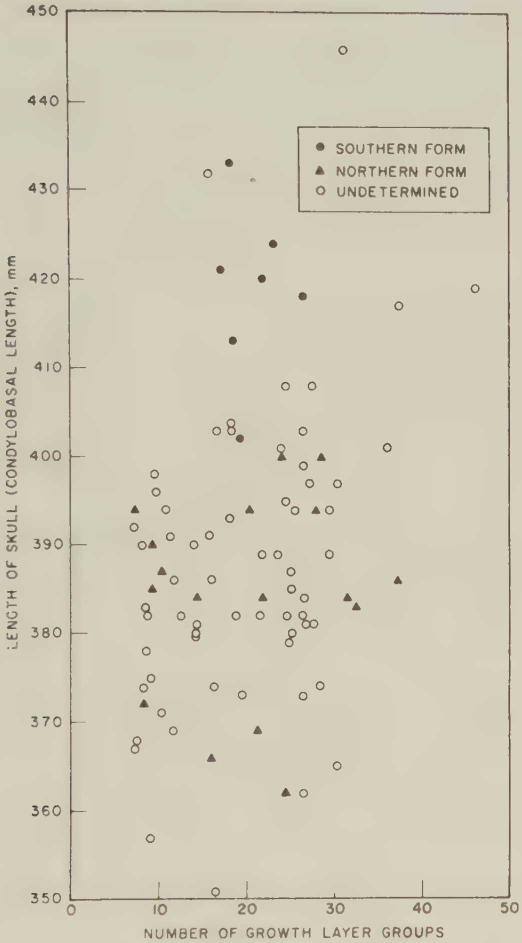

FIG. 21.4. Relationship between total length of skull (condylobasal length) and age. Southern form = specimens from south of 32°N; northern form = specimens from north of 37°N; undetermined = specimens from between 32°N and 37°N.

Reproduction

Published accounts of reproduction in *L. obliquidens* in the north-eastern Pacific are few. Since the extensive study of Harrison, Brownell, and Boice (1972), reproductive data on only four animals have appeared in the literature (Harrison and McBrearty 1977; Sawyer and Walker 1977). Perrin and Reilly (1984) recently reviewed reproductive parameters from the literature.

Based on 33 specimens (18 females and 15 males) from the Southern California Bight and a single male from Punta Abreojos, Baja California, Mexico, Harrison *et al.* (1972) noted, but were unable to explain, a considerable variability in the length at sexual maturity of either sex, or a

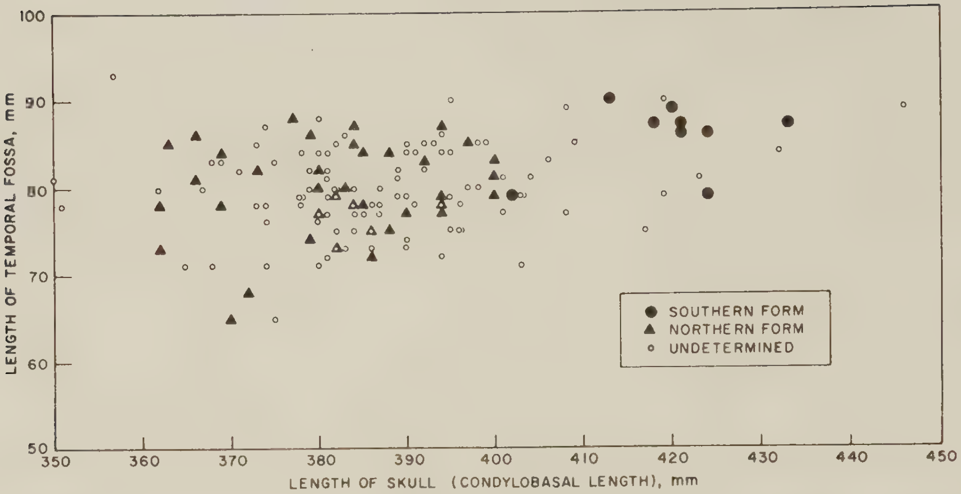

FIG. 21.5. Relationship between length of the skull (condylobasal length) and length of the temporal fossa. Southern form = specimens from south of 32°N; northern form = specimens from north of 37°N; undetermined = specimens from between 32°N and 37°N.

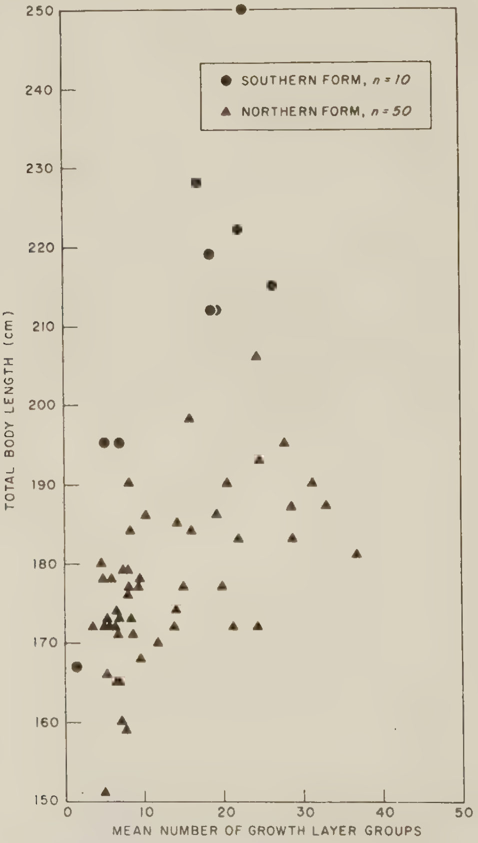

FIG. 21.6. Relationship between total body length and age. Southern form = specimens from south of 32°N; northern form = specimens from north of 37°N.

variability in body length and number of corpora of females. Data from the present sample contain comparable variability. For example, a 197 cm female estimated to be 6.9 years old had no corpora, while a 172 cm female estimated to be 24.5 years old had 23 corpora (Table 21.2), and a 179 cm male of undetermined age was sexually mature while a 213 cm male of undetermined age was sexually immature (Table 21.3). We hypothesize that such disparities relate, at least in part, to an overlap in distribution of the two populations between 32° and 37°N. Unfortunately, reproductive information available from below 32°N is insufficient to permit us to test this hypothesis.

Harrison *et al.* (1972) estimated length at birth to be about 95 cm. The largest foetus known to us was a 109 cm captive stillborn (Harrison and McBrearty 1977). Only one foetal specimen (52 cm) has been collected from the southern population. Due to the large differences in the overall size noted for the southern and northern temperate forms, using existing foetal length and length-at-birth data could lead to considerable error in estimation of foetal growth rate and gestation period.

Colouration

Pacific white-sided dolphins are strikingly marked, with a black dorsal surface, light gray sides, and a white ventrum (see Fig. 21.1). The black cape is interrupted on each side of the dorsal fin by a light stripe, originating in the light colour of the forehead and face, curving over the top of the melon, continuing along the side to below the dorsal fin, then turning downward and widening to form a prominent light gray patch on the flank. The beak is dark and a narrow stripe extending forward from the flipper is continuous with the black of the lips. The sides of the body in front of the dorsal fin and the forehead are gray. A thin dark band separates the gray and black zones of the side from the white ventrum. The dorsal fin is dark on the anterior third and light on the posterior two-thirds. The flippers are often similarly bi-coloured. The flukes are all dark.

Our impressions from numerous observations of free-ranging and captive individuals are that foetuses (Fig. 21.7) and newborn calves contain essential elements of adult colour patterns but in muted expression. The various components appear to intensify with age, and there is wide variability in component intensity even within a herd. We examined photographs of 13 known-length individuals (seven males and six females) but were unable to define any consistent patterns of variation.

Anomalous colour patterns have been observed. Brownell (1965) illustrated an animal with a black thoracic patch surrounded by exceptionally extensive and bright regions of white. A specimen so coloured was collected from 37°46′N, 124°30′W. 25 February 1966 (Fig. 21.7). Others have been seen in herds off Washington in April 1971 and off Southern California in February 1974 and 1976 (Leatherwood, unpublished observations). Brown and Norris (1956) noted three instances of what they interpreted as albinism

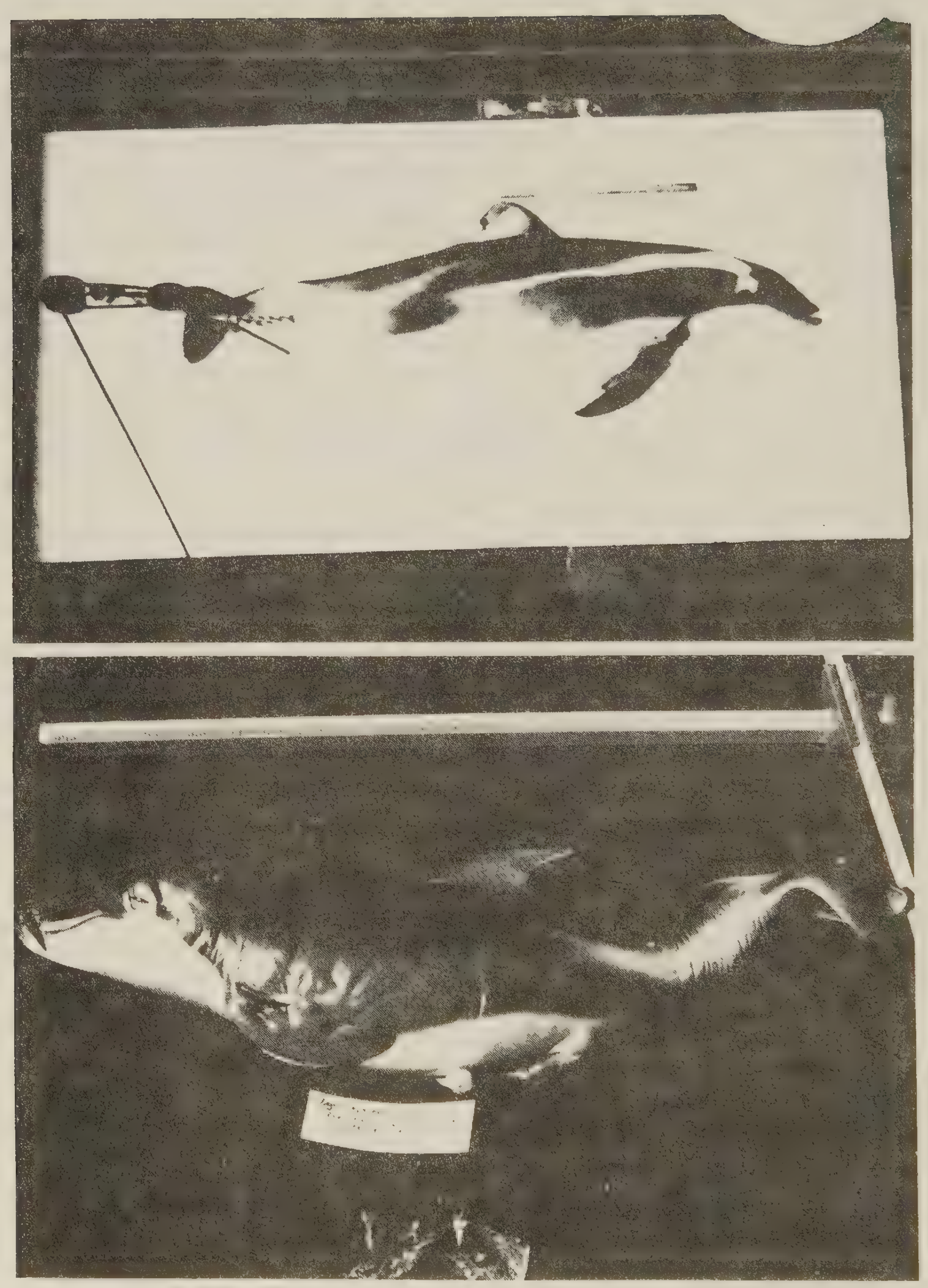

FIG. 21.7. (Top) A normally coloured foetus (Specimen MMD-1965-175, a male collected by D. W. Rice, 12 December 1965 at 32°37′N, 118°56′W). (Bottom) An anomalously coloured male (Specimen NMML 3766).

in the species, two off southern California and one off western Baja California, Mexico. Hain and Leatherwood (1982) added a report of a nearly all white individual off San Pedro Point, Santa Cruz Island in September 1968.

Food habits

Kajimura, Fiscus and Stroud (1980) and Stroud, Fiscus and Kajimura (1981) summarized food items in stomachs of Pacific white-sided dolphins from Japan, the north-western Pacific and western Bering Sea, and the west coast of North America for 1919 to 1969, and reported contents of stomachs of 44 new specimens they collected off California and Washington between 1958 and 1972. Jones (1981) summarized published accounts of stomach contents of 16 specimens from California, collected between 1958 and 1973, and added details of seven specimens he collected from beaches off northern California between 1968 and 1973. In the eastern North Pacific above Point Conception (about 34°30′N) these dolphins feed primarily on small schooling fishes and cephalopods from the epipelagic and mesopelagic zones.

Stomach contents have been reported from seven specimens collected south of Point Conception (Scheffer 1953; Brown and Norris 1956; Fitch and Brownell 1968; Kajimura *et al.* 1980; Stroud *et al.* 1981). Stomach contents from 23 additional animals collected in southern California and off Baja California, Mexico are summarized in Table 21.4. In terms of frequency of occurrence, the northern anchovy, *Engraulis mordax*, hake, *Merluccius productus*, and squid, *Loligo opalescens*, appear to be the most important prey species.

There is little information available on daily feeding cycles. Based on their observations that large stomach volumes were most often observed in animals collected before 10.00 hours, Kajimura *et al.* (1980) and Stroud *et al.* (1981) concluded that most feeding occurs at night or in the morning. Data from Jones (1981) and the present investigation are based primarily on samples from stranded specimens and shed little light on this question. Other observations, however, suggest feeding may occur at other times as well. For example, Leatherwood and Reeves (1983) reported that white-sided dolphins have been 'often seen feeding near dawn and dusk on small surfacing balls of unidentified bait.' Brown and Norris (1956), without indicating time of day, reported having many times seen these dolphins, scattered in small groups, milling around anchovy schools. Presence of numerous anchovy scales in the water on many of these occasions was taken as evidence the dolphins were feeding on anchovies. Data from a 184 cm female *L. obliquidens* radio-tagged 15 December 1972 and tracked sporadically from aircraft during daylight hours between 19 December 1972 and 26 January 1973 indicate dives during early and mid-morning (0730-1015) (Leatherwood and Evans 1979; Leatherwood, unpublished data). In the Southern California Bight, white-sided

Table 21.4. *Summary of stomach contents from 23 specimens of* Lagenorhynchus obliquidens *from Southern California and the west coast of Baja California, Mexico*

	Volume		Number		Occurrence	
Food Item	ml.	% of Total	No.	%of Total	No.	% (N=23)
TOTAL	23800	100	5469	100	—	—
FISH	23490	98.70	5184	94.90	20	86.90
Clupeidae						
Sardinops sagax	243	1.00	9	0.20	3	13.00
Engraulidae						
Engraulis mordax	17936	75.40	4212	77.00	18	78.30
Bathylagidae						
Leuroglossus stilbius	tr.	—	1	0.02	1	4.30
Myctophidae						
Diaphus theta	tr.	—	1	0.02	1	4.30
Triphoturus mexicanus	tr.	—	9	0.02	2	8.70
Batrachoididae						
Porichthys notatus	tr.	—	21	0.40	3	13.00
Porichthys myriaster	tr.	—	16	0.30	2	8.70
Ophidiidae						
Chilara taylori	tr.	—	3	0.05	2	8.70
Merlucciidae						
Merluccius productus	507	2.10	778	14.00	14	60.90
Scorpaenidae						
Sebastes sp.	tr.	1	40	0.70	3	13.00
Anoplopomatidae						
Anoplopoma fimbria	tr.	—	2	0.04	1	4.30
Carangidae						
Trachurus symmetricus	1063	4.50	55	1.00	8	34.80
Sciaenidae						
Genyonemus lineatus	tr.	—	8	0.10	1	4.30
Seriphus politus	tr.	—	2	0.04	1	4.30
Scombridae						
Pneumatophorus japonicus	3741	15.70	20	0.40	1	4.30
Stromateidae						
Peprilus simillus	tr.	—	5	0.10	2	8.70
Cynoglossidae						
Symphurus atricauda	tr.	—	1	0.02	1	4.30
Pleuronectidae						
Hypsosetta guttata	tr.	—	1	0.02	1	4.30
CEPHALOPODS	310	1.30	285	5.10	14	60.90
Loliginidae						
Loligo opalescens	310	1.30	220	4.00	13	56.50
Gonatidae						
Gonatus spp.	tr.	—	28	0.50	1	4.30
Octopoteuthidae						
Octopoteuthis sp.	tr.	—	8	0.10	3	13.00
Onychoteuthidae						
Onychoteuthis sp.	tr.	—	23	0.40	3	13.00
Octopodidae						

dolphins are sometimes caught incidentally in anchovy purse-seine operations, set in daylight and darkness. Presumably, dolphins caught were feeding on anchovies.

A white-sided dolphin captured near dawn on 9 December 1970 in an anchovy purse-seine off Point Fermin, California, was transported to Marineland of the Pacific, where it lived until 17 December 1970. Although the dolphin was fed exclusively herring, *Clupea pallasi*, during its eight day internment, the stomach was found after death to also contain otoliths of anchovies (Walker, unpublished data). This observation cautions against assuming that the contents of a dolphin's stomach represent the last feeding before death.

Parasitism and disease

The occurrence of parasites in *L. obliquidens* is summarized in Dailey and Brownell (1972) and Dailey and Walker (1978). Of the eight genera of parasites documented from this species, only the air sinus parasites, *Nasitrema* spp. (Trematoda) and *Crassicauda* sp(p). (Nematoda) have been implicated in natural mortality of small cetaceans in the eastern North Pacific (Dailey and Perrin 1973; Dailey and Walker 1978; Perrin and Powers 1980; Walker, Hochberg, and Hacker 1984).

In the present sample, specimens of *Nasitrema* were found in dolphins collected at sea from 25°22′N to 37°46′N, and specimens of *Crassicauda* were recovered in free-ranging animals from 33°40′N to 46°14′N. The evidence for the incidence and distribution of *Crassicauda* was primarily the presence of intact parasites recovered during necropsy. Incidence of infections was low, occurring in only 10% (four of 39) of the animals examined.

We also examined 197 skulls for evidence of *Crassicauda* bone lesions, described by Dailey and Perrin (1973). Only one specimen, a 160 cm juvenile female collected by W. A. Walker 26 July 1971 at 33°53′N, 118°25′W, had such lesions. The animal's left periotic bone was almost completely eroded (illustrated in Cowan, Walker, and Brownell 1985). The low rate of *Crassicauda* infection implied by the low incidence (0.5%) of bone lesions in the skull sample examined should be interpreted cautiously, as the sample was biased toward specimens of older age classes.

We examined 63 post-cranial skeletons for disease. Of these, 34 (54%) demonstrated some degree of vertebral bone disease (osteonecrosis) (Fig. 8). The extent of damage varied from necrosis and fusion of two to three adjacent vertebrae to extreme cases in which the entire lumbar region was fused and the associated vertebral centra were considerably distorted. In four instances, vertebral osteonecrosis was encountered during dissection of whole specimens. In none of the four cases was there gross evidence of pathology of adjacent muscles or integument. Examination of the data revealed no association between locality, sex, length, or age and this disease.

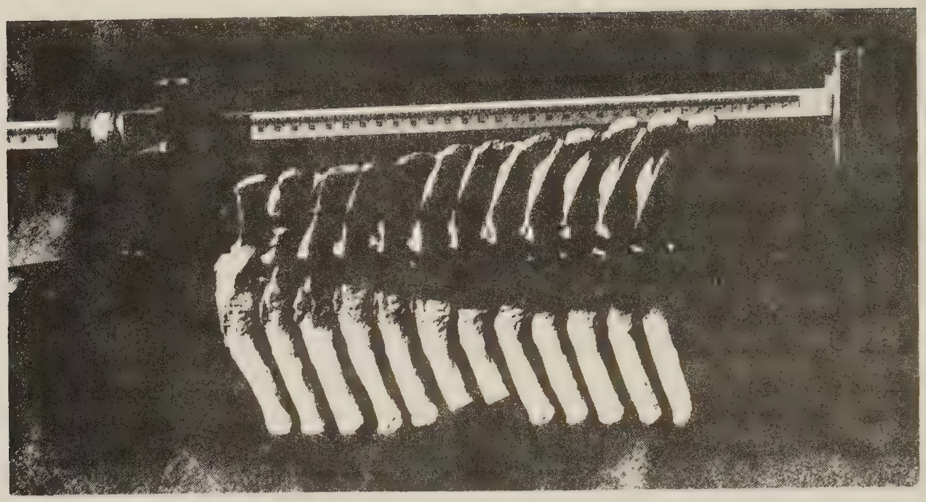

FIG. 21.8. A section of lumbar vertebrae showing osteonecrosis.

The incidence of osteonecrosis was the same in stranded animals (21 of 39 or 53.8%) and animals collected at sea (13 of 24 or 54.2%). We conclude, therefore, that this vertebral bone disease does not play a significant role in strandings. To date, the aetiology of the disease is unknown.

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86138

THE SEX RATIO AND GONAD INDICES OF SWORDFISH, *XIPHIAS GLADIUS*, CAUGHT OFF THE COAST OF SOUTHERN CALIFORNIA IN 1978

In the tropical and subtropical Pacific, swordfish, *Xiphias gladius*, about to spawn are found throughout the year but are most abundant from March to July (Palko et al. 1981). There is, however, little information on the reproductive potential of swordfish during their summer and autumn migrations into the Southern California Bight, a temperate region encompasing the principal U.S. west coast swordfish fishing grounds. In 1978 scientists from the Southwest Fisheries Center collected the gonads of swordfish harpooned in the Bight (from Point Conception to the United States-Mexico border) in order to determine sex ratios, gonad indices, and the reproductive condition of these fish.

Methods

Ninety swordfish were sampled from 25 August through 20 November 1978. After capture their gonads were preserved in 10% Formalin[1] and, in the laboratory, were weighed to the nearest gram and their sex determined visually. Ovarian sections used in the histological analysis were obtained from segments removed from the centers of the ovaries. Segments were imbedded in Paraplast and 8 μm sections were cut, stained in iron hematoxylin, and counterstained in eosin.

Two gonad indices were calculated for each pair of ovaries to permit comparisons with two existing studies on the sexual maturity of Pacific swordfish. The first (from Uchiyama and Shomura 1974) is simply the percentage of the fresh weight of the ovaries to the total weight of the fish:

$$GI = \frac{WT\text{-}O}{WT\text{-}F} \times 100 \qquad (1)$$

where GI = gonad index,
$WT\text{-}O$ = fresh weight of both ovaries, and
$WT\text{-}F$ = fresh weight of whole fish.

The second index (from Kume and Joseph 1969) is

$$GI = (W/L^3) \times 10^4 \qquad (2)$$

where GI = gonad index,
W = fresh weight of both ovaries in grams, and
L = post-orbital fork length in centimeters.

Because the gonads used in this study were preserved, and thus subject to shrinkage and loss of weight, it was necessary to estimate their fresh weight using the relationship (from Uchiyama and Shomura 1974):

$$Y = e\,\frac{\ln X - 0.155}{0.969} \qquad (3)$$

where Y = estimated fresh weight of ovaries, and
X = weight of preserved ovaries.

The estimated weight loss due to preservation was as high as 7%.

Results and Discussion

All 90 swordfish collected were mature with fork lengths ranging from 133 to 218 cm. Of these, 23 (26%) were males and 67 (74%) were females for a sex ratio of 0.34:1 (M:F). Although the proportion of females varied among months, our sample sizes were too small to demonstrate such variation.

Female swordfish in our sample all had gonad indices that were considerably lower than those of comparable studies. Uchiyama and Shomura (1974) collected 16 pairs of ovaries from swordfish caught near Hawaii and found three pairs to be ripe. These had gonad indices (from Equation (1)) of 6.4, 8.4, and 9.8 whereas our highest value (from Equations (1) and (3)) was 1.0. Kume and Joseph (1969) examined 362 pairs of ovaries from swordfish captured in the eastern Pacific (east of long. 130°W) and found two ripe specimens whose gonad indices (from Equation (2)) were 10.8 and 11.1. By comparison, the highest from our study (from Equations (2) and (3)) was 1.8. These results indicate swordfish in the Southern California Bight during our sampling period were not spawning.

A histological analysis was performed on a subset of 16 pairs of ovaries from our sample. Histological analyses can be used to determine not only if a fish is in spawning condition but, also, if it has recently spawned (Hunter and Macewicz 1985). Ovaries from our sample contained no mature oocytes and, in addition, did not contain abundant atretic oocytes indicative of the resorption process. Instead the ovaries were in the regressed stage and contained primary oocytes lining connective tissue septa. These results indicate that the swordfish were reproductively inactive during the sampling period and for at least a month or two before capture. Although this conclusion does not preclude the possibility of spawning early in the year, swordfish then are scarce. Also water temperatures favorable for spawning (Palko et al. 1981) are not widespread in the summer and autumn, and are virtually nonexistant the remainder of the year.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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EARL C. WEBER

Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
8604 La Jolla Shores Drive
La Jolla, CA 92038

STEPHEN R. GOLDBERG

Department of Biology
Whittier College
Whittier, CA 90608

86139

Mammalian metabolite flux rates in a teleost: lactate and glucose turnover in tuna

JEAN-MICHEL WEBER, RICHARD W. BRILL, AND PETER W. HOCHACHKA
Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 2A9, Canada; and Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Honolulu, Hawaii 96812

WEBER, JEAN-MICHEL, RICHARD W. BRILL, AND PETER W. HOCHACHKA. *Mammalian metabolite flux rates in a teleost: lactate and glucose turnover in tuna.* Am. J. Physiol. 250 (Regulatory Integrative Comp. Physiol. 19): R452–R458, 1986.—Lactate and glucose turnover rates were measured by bolus injection of [U-^{14}C]lactate and [6-^{3}H]glucose in cannulated lightly anesthetized skipjack tuna, *Katsuwonus pelamis.* Our goals were *1)* to find out whether the high rates of lactate clearance reported during recovery from burst swimming in tuna could be accounted for by high blood lactate fluxes; *2)* to extend the observed correlation between lactate turnover and lactate concentration in mammals to a nonmammalian system, and *3)* to assess the importance of lactate and glucose as metabolic fuels in tuna and to compare their flux rates with values reported for mammals. Measured lactate turnover rates ranged from 112 to 431 μmol·min^{-1}·kg^{-1} and were correlated with blood lactate concentration. Glucose turnover rate averaged 15.3 μmol·min^{-1}·kg^{-1}. When correcting for body mass and temperature, skipjack tuna has at least as high or even higher lactate turnover rates than those recorded for mammals. Tuna glucose turnover rate is similar to that of mammals but much higher than levels found in other teleosts. Even the highest lactate turnover rate measured in tuna cannot fully account for the rate of blood lactate clearance observed during recovery, suggesting that some of the lactate produced in skeletal muscle must be metabolized in situ. After injection of [U-^{14}C]lactate, <5% of the total blood activity was recovered in glucose, suggesting that the Cori cycle is not an important pathway of lactate metabolism in tuna.

replacement rate; carbohydrate metabolism; fish; *Katsuwonus pelamis*; scaling

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OVER THE PAST FEW YEARS, exercise physiologists and biochemists have shown renewed interest in the study of lactate with the realization that this metabolite plays a double role in muscle metabolism. It is not simply an end product of anaerobic glycolysis but also an important fuel for aerobic work (18). In mammals, muscle lactate production starts long before O_2 becomes limiting (11), and lactate turnover rate increases with blood lactate concentration (10, 12, 13, 20, 23).

As elite swimmers, tuna are characterized by a combination of endurance and sprint capabilities. Not only can they sustain moderate swimming speeds over very long distances, but they can reach top velocities of >20 body lengths/s (33). The metabolic machinery supporting tuna locomotion must meet the challenges imposed by this lifestyle, and it should include *1)* fast fluxes of fuels to the working muscles during aerobic endurance swimming and *2)* fast fluxes of anaerobic end products to their sites of catabolism during recovery from burst exercise.

While swimming at high speed, skipjack tuna can generate lactate very rapidly, up to record concentrations of 90 μmol/g in white muscle (16). During recovery, blood lactate clearance occurs much faster in tuna than in other teleosts. Minimum blood lactate concentrations are reached after <2 h of recovery in exhausted skipjacks (3). Even with a much smaller lactate load, clearance takes 12 h in rainbow trout (6).

Present views of exercise and recovery in fish rely mainly on the interpretation of metabolite concentration measurements. Estimates of metabolic fluxes would provide a new dimension to the understanding of fuel metabolism as a dynamic process. However, glucose turnover rate has only been measured in kelp bass and coho salmon (5, 26), and lactate fluxes have not been investigated in fish.

The goal of this study, therefore, was to measure lactate and glucose turnover rates in skipjack tuna to *1)* find out whether the high rate of lactate clearance reported in tuna during recovery could be accounted for by high blood lactate fluxes, *2)* extend the observed correlation between lactate turnover rate and lactate concentration in mammals to a nonmammalian species, *3)* assess the importance of lactate and glucose as metabolic fuels in a fast pelagic fish and compare their flux rates with values measured in mammals, and *4)* obtain some insight into the possible operation of the Cori cycle in tuna.

MATERIALS AND METHODS

Experimental animals. Skipjack tuna, *Katsuwonus pelamis,* were caught with barbless hooks off the coast of Oahu, HI, from May to August 1984. They were brought back to the Kewalo Research Facility (National Marine Fisheries Service, Honolulu laboratory) in the bait wells of commercial fishing vessels and transferred to 75,000-liter circular holding tanks supplied with well-aerated 25°C seawater. The fish were not fed in captivity and were used in the first 4 days after capture. The status of their carbohydrate stores was determined in a control group of five fish to assess whether capture and captivity caused glycogen or glucose depletion. The control animals were kept for 4 days in captivity under the same conditions as the fish used in turnover experiments. They were caught with a net and killed with a sharp blow on the head. A blood sample was immediately taken by cardiac puncture. Approximately 1 g of white muscle, red muscle, and liver were freeze clamped in liquid N_2 and extracted in perchloric acid by use of previously described procedures (16). Glucose, glucose 6-phosphate, and glycogen concentrations were determined in these tissues.

Fish to be used in turnover experiments swam vigorously around their holding tanks from 1 to 10 min and then were directed to a large funnel leading to a 10-liter plastic bag containing O_2-supersaturated water with MS-222 (tricaine methanesulfonate, 1:2,000, wt/vol) an effective fish anesthetic.

Catheterization. As soon as the fish stopped moving, it was brought into the laboratory and placed ventral side up on an operating table. The gills were irrigated with aerated 24°C recirculating seawater containing MS-222 (1:15,000). A catheter (Surflo I.V. Catheter 20 g × 2 in., ID 0.80 × 51 mm, Terumo, Japan) was inserted at a 45° angle ~2 cm in front of the pelvic fins, directed toward the head for the percutaneous cannulation of the ventral aorta just anterior to the heart. The catheter was connected to a pressure transducer for pressure verification of catheter position. A 40-cm piece of PE-160 was attached to the catheter and sutured to the underside of the animal. Double cannulation (ventral and dorsal aorta) was attempted on a few individuals. The dorsal aorta cannulation was done through the mouth by use of a technique described in Jones et al. (21).

Catheters, PE tubing, and syringes were always rinsed with heparinized saline (10 U/ml) before use. Total cannulation time never exceeded 20 and 35 min for single and double cannulations, respectively. Once the catheter(s) was in place, heart rate and blood pressure were monitored via the transducer. The tuna was uprighted, strapped to a Plexiglas holder, and submerged. The anesthetic concentration was then reduced to ~1:30,000 and was adjusted individually for each fish throughout the turnover experiments. The animals were slowly moving their tail without thrashing.

Preinjection measurements of heart rate and blood pressure together with blood glucose concentration were valuable indicators of the state of the animal after surgery. Animals showing a blood glucose concentration of <1 mM were not used for turnover experiments. In some cases, blood glucose concentration started to decrease after several hours. Whenever this occurred the tail ends of decay curves were not included in the analysis. After this operation, sampling times for all turnover experiments ranged from 2 to 6 h, and the assumptions of steady-state kinetics required by the bolus injection technique were met.

Injection of labeled metabolites and blood sampling. A bolus of 25–35 μCi [U-^{14}C]lactate (sp act >100 mCi/mmol), 10 μCi [U-^{14}C]glucose (4 mCi/mmol) or 25–30 μCi [6-^{3}H]glucose (300 mCi/mmol) was injected via the catheter at *time 0*. In two specimens [U-^{14}C]glucose and [6-^{3}H]glucose were injected simultaneously to estimate glucose carbon recycling. The line was flushed with 3 ml heparinized saline immediately after injection. Blood samples (0.5 ml) were drawn starting 1 min after injection to allow the bolus to equilibrate in the rapidly mixing pool. Samples were drawn about every 40 s during the first 5 min and then at appropriate intervals. The catheter was flushed with 0.5 ml saline between samples. The amount of blood drawn throughout an experiment never exceeded 10% of total blood volume. Radiochemicals were purchased from New England Nuclear (Boston, MA) and Amersham (Oakville, Ontario).

Metabolite assays and counting. Blood samples were deproteinized immediately in 1–2 parts cold perchloric acid (8%) and spun down. The supernatant was stored at −4°C. Lactate and glucose concentrations were determined enzymatically at 340 nm following the procedure of Bergmeyer (4). Tissue glycogen of the control fish was determined by the amyloglucosidase hydrolysis technique (4). All metabolite assays were performed in duplicate, at the latest 7 days after sampling.

Blood glucose was separated to determine its activity. Blood perchloric acid extract (200 μl) was incubated with 4 ml 1 M glucose and 0.6 g Amberlite MB-3 resin (Sigma, St. Louis, MO). The mixture was shaken for 2 h at 25°C, allowing all the charged compounds to bind to the resin. The resin was then spun down, and 1 ml of the supernatant was counted. After separation 90.1% of the total glucose was recovered as determined with [6-^{3}H]glucose standards.

Lactate activity was measured by counting 40 μl perchloric acid extract and correcting for the activity found in glucose. Scintillation counting was performed on a Beckman LS-9000 by use of an external standard quench correction system. All samples were mixed with 10 ml aqueous counting scintillant II (Amersham) and left in the dark for at least 12 h before counting. Single-label counting showed an efficiency of 94% for ^{14}C and 42% for ^{3}H (dual label: 73 and 35%, respectively).

Calculations and statistics. Under steady-state conditions the rate of appearance equals the rate of utilization and is called turnover rate. Measurements of turnover rate by the bolus injection technique requires steady-state metabolite concentration because the rate of appearance and the rate of utilization cannot be estimated separately. In this study, turnover rate was calculated as the dose injected (in dpm) divided by the surface area under the specific activity decay curve [in $\text{dpm} \cdot \mu\text{mol}^{-1} \cdot \text{min}^{-1}$, see Katz et al.(23)]. To calculate this surface area the decay curve was first fitted with a multiexponential function by use of the nonlinear regression program P3R from BioMedical Data Processing (BMDP) (35), which determines the least-squares estimates of the function parameters by a modified Gauss-Newton algorithm. The fitted function was then integrated between *time 0* and the time when 5% of the maximum possible specific activity was reached. The maximum possible activity was calculated as the dose injected divided by the volume of the rapidly mixing pool estimated to be 8% of the body volume. Metabolic clearance rate (MCR) was calculated as turnover rate divided by the steady-state metabolite concentration (23).

RESULTS

Glucose, glucose 6-phosphate, and glycogen concentrations in tissues of animals from the control group are given in Table 1. Skipjack tuna blood glucose concentration appeared to be regulated because it was relatively constant throughout the turnover experiments (Tables 2 and 3, Fig. 3*B*). However, the set point was different between individuals, and the mean blood glucose concentration ranged from 1.2 to 6.8 mM. In each turnover experiment a blood sample was drawn before injection of the radioactive bolus. Lactate and glucose concentrations of the preinjection sample were always within 2% of the means given in Tables 2 and 3.

Lactate turnover. After injection of [U-^{14}C]lactate the activity recovered in glucose never exceeded 5% of total blood activity, even after 6 h. The lactate specific activity decay curves were best fitted with three exponential functions (Fig. 1A). In all cases the calculated functions fitted the observed values extremely well. *Fish 4* had a relatively low blood lactate concentration and the lowest turnover rate. Specific activity decreased sharply over the first 10 min after injection and then more gradually (Fig. 1*A*). Blood lactate concentration was relatively stable throughout the experiment (Fig. 1B).

Turnover rates and MCR are given for seven individuals in Table 2. These animals were selected because the coefficient of variation of their mean blood lactate concentration was <15%. These seven individuals had stable enough lactate concentrations to justify the use of steady-state kinetics in our calculations. Mean blood lactate concentrations in individual fish ranged from 10.2 to 27.6 mM. Turnover rate was positively correlated with lactate concentration (Fig. 2), and the slope was highly significantly different from zero ($F = 40$, $P < 0.001$, 1 df/7 df, ANOVA).

TABLE 1. *Tissue metabolite concentrations in control group of skipjack tuna*

Tissue	Glucose	Glucose 6-Phosphate	Glycogen, Glucosyl Units
White muscle, μmol/g wet wt	0.68±0.12	4.16±0.97	92.54±9.17
Red muscle, μmol/g wet wt	0.84±0.17	1.30±0.34	24.22±5.20
Liver, μmol/g wet wt	3.54±0.34		4.06±0.87
Blood, μmol/ml	3.04±0.39		

Values are means ± SE for 5 fish. Animals were handled and kept in captivity under same conditions as tuna used in turnover experiments.

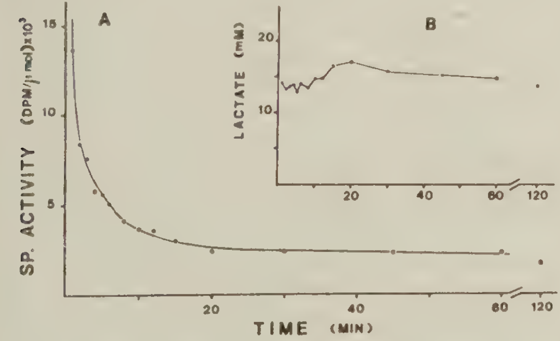

FIG. 1. Lactate turnover rate measurement in skipjack tuna (*fish 4*). Radioactive bolus injected and blood sampled via ventral aorta catheter. *A*: blood lactate specific activity decay curve after injection of 25 μCi [U-^{14}C]lactate at *time 0*. Curve fitted with sum of 3 exponential functions. *B*: blood lactate concentration during sampling period.

TABLE 2. *Blood metabolite concentrations and rate of lactate turnover in skipjack tuna*

Fish No.	Sampling Site	Wt, g	Glucose, mM	Lactate, mM	*n*	Lactate Turnover Rate, μmol·min⁻¹·kg⁻¹	Metabolic Clearance Rate, ml·min⁻¹·kg⁻¹
1	VA	1,065	4.35±0.08	27.5±1.0	11	380.9	13.9
2	VA	1,298	4.26±0.12	25.0±0.4	13	296.0	11.8
3	VA	1,440	2.30±0.07	19.1±0.5	12	299.8	15.7
4	VA	1,436	6.31±0.14	14.6±0.3	15	112.6	7.7
5	VA	1,880	1.85±0.03	12.0±0.5	13	199.9	16.7
6	VA	1,405	4.10±0.11	11.6±0.3	11	180.8	15.6
	DA		4.12±0.09	10.2±0.4	11	131.8	12.9
7	VA	1,412	1.23±0.02	26.5±0.3	10	415.2	15.7
	DA		1.22±0.02	27.6±0.5	11	431.4	15.6

Values are means ± SE. *n*, number of blood samples; VA, ventral aorta; DA, dorsal aorta. *Fish 6* and *7* were sampled simultaneously from VA and DA. Turnover rate was determined by bolus injection of [U-^{14}C]lactate.

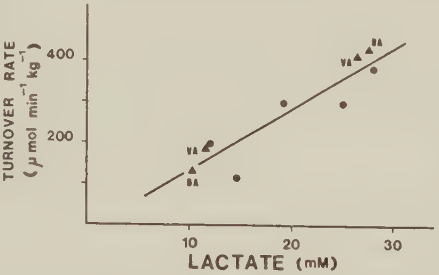

FIG. 2. Relationship between lactate turnover rate and blood lactate concentration in skipjack tuna. *Circles*, animals with single ventral aorta catheter; *triangles*, 2 animals (*fish 6* and *7*) sampled simultaneously from ventral aorta (VA) and dorsal aorta (DA). Line was fitted by linear regression (slope = 15.1, $r^2 = 0.85$).

MCR was not affected by blood lactate concentration. A linear regression for blood lactate concentration vs. MCR (graph not shown) had a slope of 0.044 ($r^2 = 0.0134$), which is not significantly different from zero ($F = 0$, $P > 0.5$, 1 df/7 df, ANOVA). Mean MCR was 14.0 ± 0.9 (SE) ml·min^{-1}·kg^{-1} ($n = 9$).

Simultaneous sampling from the dorsal aorta and the ventral aorta was performed on *fish 6* and *7*. Turnover rates determined from both sampling sites were similar (Table 2, Fig. 2), indicating that these two sites could be used interchangeably. Differences between the dorsal aorta and ventral aorta lactate specific activity decay curves did not allow us to quantify lactate utilization by the gills.

Glucose turnover. As in mammalian species, the turnover rate for glucose was much lower than for lactate. A typical specific activity decay curve is given for *fish 9* (Fig. 3*A*), which exhibited an average turnover rate. The decay curves for glucose were best fitted with the sum of two exponential functions. Turnover rate and MCR for

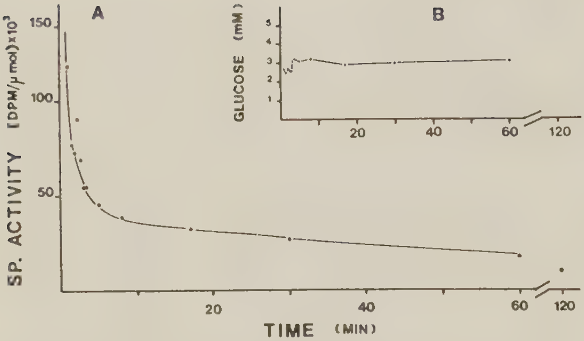

FIG. 3. Glucose turnover rate measurement in skipjack tuna (*fish 9*). Injection and blood sampling are same as Fig. 1. *A*: blood glucose specific activity after injection of 28.2 μCi [6-^{3}H]glucose at *time 0*. Curve fitted with sum of 2 exponential functions. *B*: blood glucose concentration during sampling period.

TABLE 3. *Blood glucose concentration and turnover rate in skipjack tuna*

Fish No.	Wt, g	Label	Glucose, mM	*n*	Glucose Turnover Rate, μmol·min^{-1}·kg^{-1}	Metabolic Clearance Rate, ml·min^{-1}·kg^{-1}
8	1,680	^{3}H	2.52±0.08	11	14.8	5.9
9	1,497	^{3}H	2.83±0.09	13	15.2	5.4
10	1,320	^{3}H	6.77±0.17	13	11.0	1.6
11	1,671	^{3}H	2.46±0.03	11	17.3	7.0
		^{14}C			12.5	5.1
12	1,597	^{3}H	5.19±0.10	13	18.1	3.5
		^{14}C			15.2	2.9

Values are means ± SE. *n*, number of blood samples. Turnover rates were determined by bolus injection of [6-^{3}H]glucose or [U-^{14}C]glucose. *Fish 11* and *12* were injected with both isotopes. Injection of radioactive bolus and blood sampling were done via ventral aorta catheters.

glucose are given in Table 3. Turnover rate was independent of glucose concentration ($F = 1$, $P > 0.25$, 1 df/3 df, ANOVA) and averaged 15.3 ± 1.2 (SE) μmol·min^{-1}·kg^{-1} as determined with [6-^{3}H]glucose ($n = 5$). MCR was 4.7 ± 1.0 (SE) ml·min^{-1}·kg^{-1} ($n = 5$). *Fish 10* and *12* showed a high blood glucose concentration, but their turnover rate was not elevated. Consequently, glucose MCR was lower than average for these two fish.

[6-^{3}H]glucose is considered an irreversible tracer because its predominant end product is tritiated H_2O. The reincorporation of labeled water into glucose is insignificant because rapid equilibration occurs within the large amount of body H_2O. [U-^{14}C]glucose is a reversible tracer because ^{14}C incorporated into other metabolic intermediates can be recycled back to glucose. This recycling slows down the decay of the specific activity curve, causing an underestimation of the true rate of glucose turnover. In this study, turnover rate determined with [6-^{3}H]glucose was much higher than with [U-^{14}C]glucose (Table 3), indicating that glucose carbon recycling is relatively high in tuna (28 and 16% for *fish 11* and *12*, respectively).

DISCUSSION

The lactate turnover rates reported here for skipjack tuna range from 112 to 431 μmol·min^{-1}·kg^{-1}. These values are higher than the rates reported by Okajima et al. (28) for resting rats (70 μmol·min^{-1}·kg^{-1}) and are comparable to values obtained at rest (200 μmol·min^{-1}·kg^{-1}) and different levels of exercise (up to 500 μmol·min^{-1}·kg^{-1}) by Donovan and Brooks (12), also in rats.

The animals used in this study were not overly stressed by capture, transportation, and short-term captivity without food. They were not exhausted because their carbohydrate stores were far from being depleted. Red muscle glycogen concentration was only 30% lower than in the group of resting skipjack tuna reported by Guppy et al. (16); white muscle concentration was 90% higher. Glucose and glucose 6-phosphate levels in the two muscle types were similar to the resting fish of Guppy et al. (16). Surprisingly, liver glycogen concentrations were low compared with other teleosts, but no other values are available for tuna liver. There is no doubt that the experimental situation used in our measurements was very artificial because the animals were restrained and lightly anesthetized. However, fish treated with MS-222 do not show any changes in blood glucose and lactate concentrations compared with untreated individuals (34). The same anesthetic causes a reduction in the levels of circulating catecholamines (27), suggesting a possible depression of carbohydrate metabolism. Until now, all attempts to carry out this type of experiment on unanesthetized free-swimming tuna have been unsuccessful.

It is important to realize that metabolite turnover rates generally depend on several critical factors that should be taken into account if meaningful comparisons are to be made, particularly with mammalian values. To begin with, the effects of exercise, body mass, and temperature will be considered in some detail. Then the possible mechanisms allowing tuna to support such high turnover rates will be discussed.

Lactate turnover rate has been shown to be positively correlated with blood lactate concentration in resting rats (28) and in resting dogs infused with different lactate concentrations (13). Turnover rate also increases with exercise intensity (10, 12, 20), but this effect is twofold because both perfusion and blood lactate concentration increase as work rate goes up. This paper shows that lactate turnover rate is also correlated with blood lactate concentration in tuna (Fig. 2), and this is the first time such a demonstration is made for a nonmammalian species. Measurements of heart rate and blood pressure (results not shown) made before the bolus injections indicate that perfusion was probably similar between individuals showing different steady-state blood lactate concentrations. Unfortunately, these measurements were not made throughout the turnover experiments, and cardiac output may have differed between individuals. However, MCR was not correlated with lactate concentration. When studying exercising animals a positive correlation between MCR and work rate would indicate different perfusion rates between different levels of exercise. Therefore, the constancy of MCR over our observed range of lactate concentrations also suggests that the relationship shown in Fig. 2 probably represents the true effect of lactate concentration independent of perfusion rate. The respective contributions of lactate concentration and perfusion rate on turnover increase should be investigated separately.

The relationship between body mass and whole-body lactate turnover (R_t, in μmol·min^{-1}) is presented for a few mammalian species in Fig. 4. A linear regression across the turnover rates of resting mammals (circles) has been drawn (slope = 0.64, $r^2 = 0.85$). The correlation is not better because it is difficult to standardize resting conditions for a wide range of body shapes and sizes, knowing that lactate production and removal rates are influenced by activity. Furthermore, lactate R_t measurements are not available for many species. The effect of exercise on turnover rate is also illustrated for rat, dog, and humans (triangles in Fig. 4). The range of values obtained for skipjack tuna in 25°C water is also plotted. These values fall well within mammalian rates even without considering the effect of temperature.

Ocean-caught skipjack tuna can have a core temperature 10°C higher than ambient, but such a high difference is only observed after feeding frenzies at sea. Captive animals subjected to violent exercise do not show more than a 5°C excess core temperature (31). It is very unlikely that the body temperature of the fish used in this study exceeded water temperature by >2–3°C. If we assume a Q_{10} of 2, the lactate turnover rates measured at 25°C should approximately double at 37°C.

It is interesting to notice that, even with a high lactate turnover rate of 400 μmol·min^{-1}·kg^{-1}, an exhausted tuna with 1 kg of white muscle at a lactate concentration of 90 μmol/g (16) would take >3 h to metabolize its lactate load of 90 mmol. However, complete recovery appears to be achieved in <2 h (3). Also, one of our cannulated animals showed a drop in blood lactate concentration from 32 to 12 mM in <2 h. These observations suggest that not all lactate passes via the blood compartment during recovery but that a significant portion is metabolized directly in white muscle.

How can a tuna turn over lactate at the same rate or faster than a 37°C mammal? Perfusion is lower in a 2-kg tuna [cardiac output of ~90 ml/min (7)] than in a mammal of similar size. Blood lactate concentration is higher in tuna, allowing faster diffusion between blood- and lactate-utilizing tissues. However, this diffusional advantage cannot fully compensate for the effect of a 10°C difference in body temperature. Therefore, tuna must have other adaptations allowing them to cycle lactate as fast as they do. The very high aerobic potential of lactate-utilizing tissues, such as red muscle (16), could allow fast lactate diffusion by maintaining a steep concentration gradient between the blood and this "lactate sink." A second possibility involves use of the central vascular countercurrent heat exchanger to accelerate movements between lactate-producing white muscle and lactate-oxidizing red muscle (P. W. Hochachka, R. W. Brill, J.-M. Weber, B. Emmett, C. Daxboeck, S. Perry, and T. W. Moon, unpublished observations).

Tuna appear to regulate their blood glucose concentration much more tightly than other teleosts (Tables 2 and 3, Fig. 3). Cannulated kelp bass (5) and rainbow trout (Weber, unpublished observations) show wide fluctuations in blood glucose levels. Tuna and mammalian insulins demonstrate similar properties (25), which may allow these fish to achieve glucose homeostasis. Even though each tuna maintained a steady blood glucose concentration, the set points ranged from 1.2 to 6.8 mM in different individuals. The significance of these observed differences is not clear but may represent different nutritional states.

Glucose turnover rate has only been measured in two other fish species. Bever et al. (5) showed that kelp bass, *Paralabrax* sp., has a rate of ~2 μmol·min^{-1}·kg^{-1}. A similar value was found for coho salmon, *Oncorhynchus kisutch* (26). The rates measured in fish species other than tuna are ~1/30 those found in resting rats (22).

Although the data base is very restricted for fish, mammalian values are available for a wide range of body sizes. The relationship between body mass and whole-body glucose turnover at rest (R_t, in μmol·min^{-1}) is

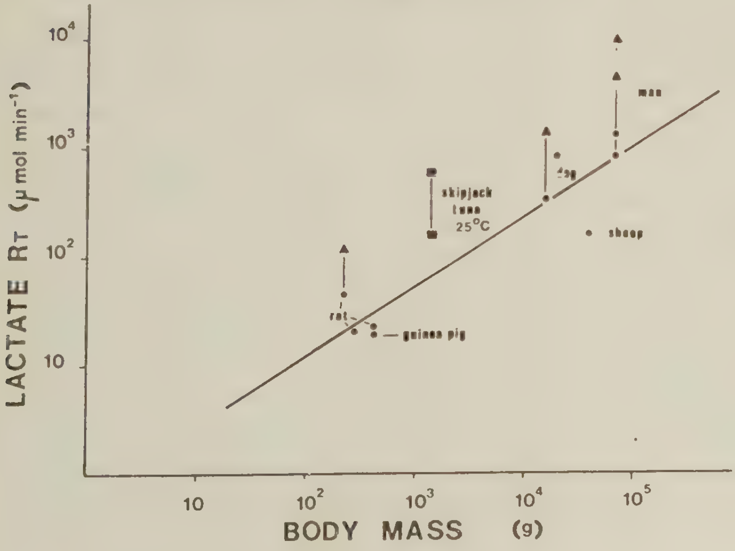

FIG. 4. Relationship between body mass and whole-body lactate turnover rate (R_t) on log-log plot for mammals and skipjack tuna. Mammals are at rest (*circles*) and exercising (*triangles*). Line fitted by linear regression using resting values for mammals only. Turnover rates measured with [^{14}C]lactate in all cases. References: rat (12, 15, 28), guinea pig (15), dog (13, 20), sheep (29) and humans (10, 30).

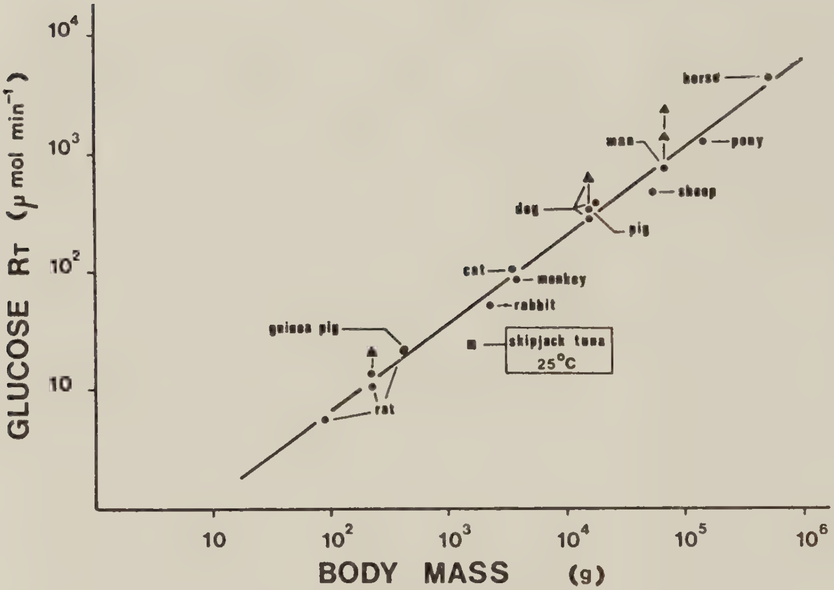

FIG. 5. Relationship between body mass and whole-body glucose turnover rate (R_t) on log-log plot for mammals and skipjack tuna. Same symbols as in Fig. 4. Linear regression fitted for resting mammals only. Turnover rates determined with [^{3}H]glucose in all cases except for horse (^{14}C). References: rat (9, 15, 22, 24), guinea pig (15), rabbit (22), cat (24), monkey (2), dog (19, 20), pig (32), sheep (8), humans (17), pony (1), horse (14).

presented in Fig. 5 on a double logarithmic scale (slope = 0.72, $r^2 = 0.99$, linear regression). Interestingly, this slope is not significantly different from the slope found for the classic body mass vs. metabolic rate relationship. The same analogy can be drawn for body mass vs. mass-specific glucose turnover rate (in μmol·min^{-1}·kg^{-1}, graph not shown, slope = −0.27, $r^2 = 0.94$). The close correlations obtained suggest that it is of minimal importance to directly measure resting glucose turnover rate in mammals unless there are good reasons to predict that the species under study will depart from this line (extremely sluggish organism or elite animal athlete) When corrected for temperature the mean glucose R_t found for tuna falls on the mammalian line. The effect of exercise on glucose R_t in mammals (triangles in Fig. 5) is much less pronounced than on lactate R_t (Fig. 4).

Under our experimental conditions very little labeled lactate was converted to blood glucose, indicating that the role played by the Cori cycle in tuna lactate metabolism is not important. It is not clear why glucose recycling was so high nor with what other compounds glucose may have been exchanging.

In conclusion, this study shows that skipjack tuna can support lactate and glucose turnover rates at least as high as those reported for mammalian species. Glucose is turned over much faster in tuna than in other teleosts, probably as a consequence of their high metabolic rate. Tuna lactate turnover rates are higher than values measured in mammals, and they are correlated with lactate concentration. These fish may be able to achieve such high turnover rates because they evolved particular anatomic and enzymatic adaptations for high-performance swimming. These high values, however, cannot fully account for the reported rates of lactate clearance during recovery, suggesting that part of the lactate produced in white muscle is metabolized in situ. The Cori cycle is probably not an important pathway for lactate clearance in tuna.

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Address for reprint requests: J. M. Weber, UBC Zoology, 6270 University Blvd., Vancouver, British Columbia V6T 2A9, Canada.

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86140

A NEW METHOD FOR ESTIMATING GROWTH AND MORTALITY PARAMETERS FROM LENGTH-FREQUENCY DATA

by

Jerry A. Wetherall
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii, U.S.A. 96822-2396

A new, simple method has been found to estimate the asymptotic length (L_∞) and the ratio of the coefficients of mortality and growth (Z/K) using only length-frequency data from a fish catch. Theoretical details of the method are given in a paper by J.A. Wetherall, J.J. Polovina, and S. Ralston, to appear in the forthcoming ICLARM proceedings of the 1985 Sicily conference on length-based stock assessment (See Fishbyte 3(1), March 1985). A practical user's guide to the new procedure, with computational algorithms and Turbo Pascal code, will be available soon from the author. In this report only a brief description of the method is given. (see also Pauly, this issue).

The sampled fish population is assumed to be stable, with constant annual recruitment, von Bertalanffy growth, and continuous mortality occurring at a uniform, instantaneous rate. A random sample of n fish are measured, m of these longer than a particular knife-edge selection length. The measurements are retained for analysis, and data on fish shorter than the selection length are neglected. In practice the assumptions on recruitment, growth, mortality and size selection are rarely satisfied. But if they are roughly true, or if corrective steps are taken during analysis, the method provides estimates that are useful for many tropical fishery management decisions and which are superior to estimates produced by other simple procedures.

With the above assumptions, it is shown in the Sicily paper that the mean length of the m selected fish ($\bar{L}$) is a linear function of the knife-edge selection length (L_c):

$$L = L_\infty \left(\frac{1}{1+\theta}\right) + L_c\left(\frac{1}{1+\theta}\right) \tag{1}$$

where $\theta = Z/K$, Z is the instantaneous morrality rate, and K and L_∞ are the growth coefficient and asymptotic length of the von Bertalanffy model.

Equation (1) is the basis of Beverton and Holt's well-known method of estimating θ given L_∞., L_c and $\bar{L}$. Rearrangement of (1) results in their classic formula

$$\theta = \frac{L_\infty - \bar{L}}{\bar{L} - L_c} \tag{2}$$

The new approach improves on the Beverton-Holt method, allowing the estimation of L_∞ in addition to θ. It does this by making fuller use of information in the sample besides the overall mean length. Specifically, it takes advantage of the linear relationship between sample mean length and the selection length.

For a series of p arbitrary cutoff lengths within the size range of the m selected fish, we construct a corresponding series of partially overlapping subsamples. The i-th subsample consists of those m_i fish whose lengths exceed L_{ci} $(i=1,\ldots,p)$. If the mean lengths for the subsamples are plotted against the cutoff lengths, a positive linear relationship results, as predicted by formula (1). For clarity, we label the intercept and slope of the straight line with conventional symbols:

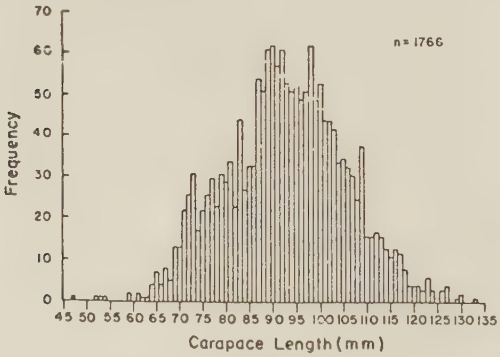

Fig. 1. Length-frequency distribution for male *Panulirus marginatus* on Maro Reef, Northwestern Hawaiian Islands.

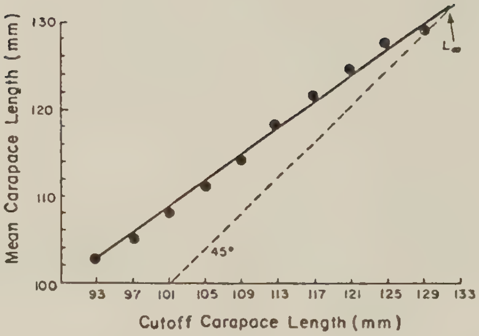

Fig. 2. Regression of mean carapace length on cutoff carapace length for 10 lobster subsamples.

$$\alpha = \left(\frac{L_\infty}{1+\theta}\right) \tag{3}$$

and

$$\beta = \left(\frac{\theta}{1+\theta}\right) \tag{4}$$

The parameters of interest, L_∞ and θ, can be estimated in two simple steps:

Step 1. Compute α and β from a linear regression of $\bar{L}_i$ on L_{ci}. Statistical weights should be used. It will usually suffice to weight each subsample mean length by the reciprocal of its variance, or even by the corresponding subsample size.

Step 2. Given the estimates of α and β, compute L_∞ and θ as the solution of Equations (3) and (4):

$$L_{oo} = \left(\frac{\alpha}{1-\beta}\right) \tag{5}$$

and

$$\theta = \left(\frac{\beta}{1-\beta}\right) \tag{6}$$

The standard errors of the estimates of L_∞ and θ can be calculated using methods discussed in the Sicily conference paper.

Figures 1 and 2 show an example, based on male spiny lobsters, Panulirus marginatus, taken in 1977 on Maro Reef in the Northwestern Hawaiian Islands (data compliments of J.J. Polovina, Honolulu Laboratory). Out of the entire sample of 1,766 lobsters, 904 lobsters had a carapace longer than the assumed knife-edge selection length of 93 mm. Measurements from these lobsters were partitioned into 10 overlapping subsamples, based on arbitrary cutoff lengths of 93 mm, 97 mm, 101 mm, 105, ..., 129 mm. The linear regression was run using reciprocals of the variances of subsample means as statistical weights. Estimates of the intercept and slope were $\alpha = 0.251$ mm and $\beta = 0.743$ mm^{-1}. Step 2 yielded the final results, $L_\infty = 131.1$ mm and $\theta = 2.89$.

86141

Problems in Assessing the Pelagic Armorhead Stock on the Central North Pacific Seamounts

JERRY A. WETHERALL
MARIAN Y. Y. YONG
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96822-2396

ABSTRACT

In this paper we examine catch and effort statistics from Japanese stern trawlers harvesting pelagic armorhead, *Pseudopentaceros wheeleri*, on the central North Pacific seamounts, and consider problems in using them to assess the armorhead stock. We begin by reviewing trends in the fishery. Next, we adopt a set of tentative assumptions about armorhead life history and population biology, and describe a nonlinear autoregressive model of armorhead stock changes based on the catch and effort data.

Trial applications of the model are then discussed. These were hampered by the unavailability of crucial data on Soviet armorhead catches, by technical difficulties in parameter estimation arising from statistical properties of the model, and by model misspecification. Despite these setbacks in applying the model, a cursory visual analysis of the Japanese trawl fishery statistics was ventured. This suggested that high variability in recruitment was probably the chief cause of fluctuations in fishing success through the mid-1970's. Further, it indicated that the collapse of the Japanese fishery in 1978 and subsequent years could not easily be ascribed to excessive trawling effort by Japanese vessels. Although the steady decline in armorhead catch per unit of effort (CPUE) reported by Japanese trawlers after 1972 was inversely correlated with their trawling effort, the behavior of the fishery in earlier years suggested that stock-independent factors may have played a more prominent role in armorhead recruitment.

Soviet catch summaries just recently made available (after the analysis of Japanese data was completed, and this manuscript first drafted) support some conclusions based on Japanese data alone. In particular, they indicate that recruitment fluctuations were largely independent of stock size during the early 1970's. However, they also show that Soviet catches were roughly five times larger than Japanese harvests during this period, suggesting that in later years, for which Soviet data are still unavailable, excessive fishing effort may indeed have played a role in the stock decline. Without a more complete and detailed Soviet record, especially during the period of stock collapse, the effects of exploitation cannot be estimated reliably.

Regardless of the causative factor, the present armorhead spawning stock is apparently at a very low level, and average recruitment may now be stock-limited. Therefore a sharp reduction in fishing mortality may be worth considering as a means to accelerate the stock's recovery.

TRENDS IN THE ARMORHEAD FISHERY

The history of armorhead fishing on the seamounts of the Emperor-Hawaiian Ridge was summarized by Takahashi and Sasaki (1977). According to their account, the resource was discovered by the Soviets in late 1967, and harvested by Russian trawlers for at least a few years. Sakiura (1972) reported that the Russian fleet took 133,400 metric tons (MT) in 1969 alone.

Unfortunately, when our analysis was done, and this paper initially drafted, there was no available record of the extent of Soviet fishing on the seamounts after 1969. However, Soviet research vessels were known to have visited the seamounts in 1976 and Japanese vessels had reported sighting Soviet trawlers operating on the seamounts. Very recently a report by the Soviet scientist Borets has become available which shows that the Soviet trawlers actually made very large catches of armorhead on the seamounts during the mid-1970's (see Boehlert 1986). Between 1968 and 1975, they caught roughly 730,000 MT, about five times the Japanese catch during the same period.

Japanese stern trawling began in August 1969 on the Kimmei Seamounts and the following month on Milwaukee Seamounts, and by the end of 1970 had spread to more southerly seamounts, including Colahan, C-H, and Hancock.[1] Nominal effort, measured in hours of trawling, has fluctuated greatly, particularly on Kimmei and Milwaukee, which have received the heaviest fishing pressure (Table 1; Fig. 1).

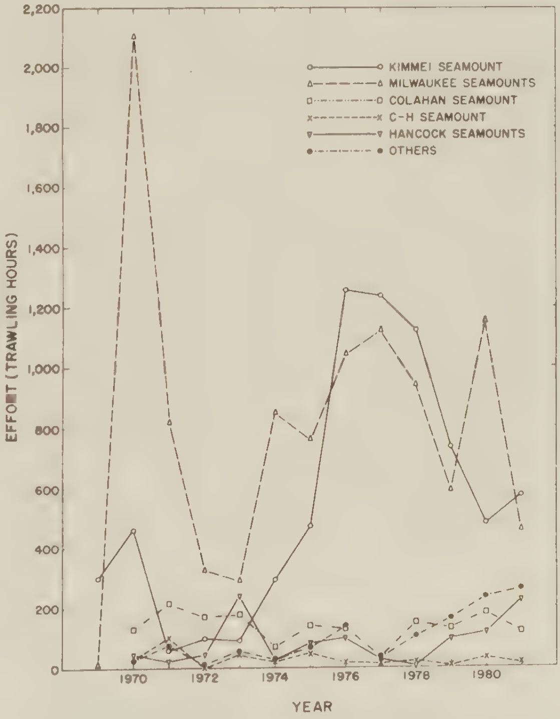

Figure 1.—Annual effort of Japanese trawlers on central North Pacific seamounts (by calendar year).

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[1] Statistics on the Japanese trawl fishery were kindly provided by Takashi Sasaki of the Far Seas Fisheries Research Laboratory, Shimizu.

Likewise, the Japanese armorhead catch has been extremely variable, with about a 10-fold range on most seamounts during the early and mid-1970's (Table 1; Fig. 2). The peak aggregate catches of armorhead by Japanese trawlers were 34,825 MT in calendar year 1972 and 28,356 MT in 1973. (By comparison, the recent summary of Soviet catch statistics shows that Soviet vessels took about 98,000 MT in 1972 and 170,000 MT in 1973.) Despite relatively steady or increasing nominal effort, the Japanese armorhead catch on all seamounts declined sharply after 1976.

The catch per unit of effort (CPUE, in metric tons per hour of trawling) for Japanese vessels decreased on all seamounts during 1969-71, then increased everywhere in 1972, in some cases by a factor of 10 or 20. Beginning in 1973 or 1974 the general trend of CPUE turned downward, and catch rates for armorhead have been severely depressed at all seamounts since 1978 (Fig. 3). This is particularly so at Milwaukee and Kimmei. However, we note that since 1978 the dominant species in the trawl catches has been the alfonsin, *Beryx splendens*, previously only a minor constituent. The CPUE for this species has greatly increased during this period, suggesting either an upsurge in abundance of alfonsin or a switching of target species. If the latter is true, then the Japanese armorhead CPUE's during recent years may exaggerate the decline in the armorhead stock.

Although the Soviet statistics were not included in the modeling and analysis reported here, it is instructive to compare them with the Japanese data *post facto*, particularly to see if CPUE data show the same trends. If we look at annual statistics, the only discrepancy between the Japanese and Soviet CPUE trends is during the period 1969-71, when it appears the fishing power of Japanese trawlers was relatively low compared with later years, or Soviet fishing power relatively high. Both sets of statistics indicate an overall decline in armorhead abundance or availability from 1969 to 1971, a substantial increase in 1972, and a steady decline through 1975 (see data in Boehlert 1986).

Length-frequency statistics from the Japanese trawl catches show that the fishery harvests only a narrow size range of armorhead, generally from about 25 to 35 cm fork length (FL). Individuals of this size are thought to be 2 to 3 years old and sexually mature (see below). Apparently the fishable stock consists almost entirely of recruits, there being few survivors from earlier year classes. The length distributions are remarkably similar on the various seamounts, and vary little from year to year. However, two noticeable changes in the length distributions have occurred. In 1972, when CPUE rose dramatically on all seamounts, the length distribution shifted downwards by about 2 cm. This was especially clear at Milwaukee and Colahan, where the largest samples of armorhead were measured (length-frequency distributions for Milwaukee are given in Fig. 4). More typical distributions were seen the following several years. Then beginning in 1978, when CPUE dropped sharply, the distributions shifted upwards on most seamounts, and broadened. If one assumes no alteration in maturation schedules, the length-frequency shifts could be taken as evidence of density-dependent growth in the pre-recruit stage. Alternatively, if growth rates have been constant, the inverse relationship between mean length of the recruits

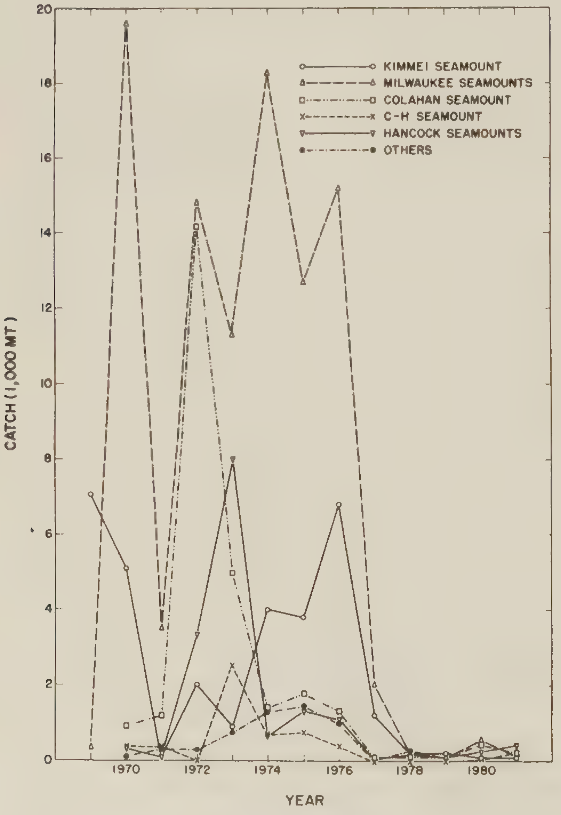

Figure 2.—Annual pelagic armorhead catch by Japanese trawlers on central North Pacific seamounts (by calendar year).

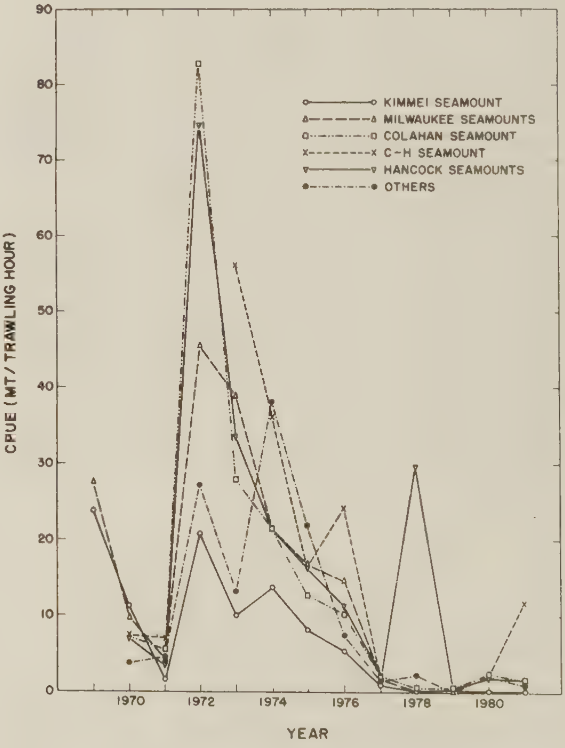

Figure 3.—Annual pelagic armorhead catch per unit of effort (CPUE) for Japanese trawlers on central North Pacific seamounts (by calendar year).

and CPUE may reflect differences in rate of maturation. The latter explanation seems less likely. However, without information on the age composition of the armorhead catches no reliable interpretations can be made.

The annual variability in armorhead CPUE is illustrated by Figure 5, in which yearly CPUE values are expressed as a proportion of the 1981 CPUE at each seamount. Peak CPUE values were in some cases two orders of magnitude greater than in the 1981 index period. Such high variability in abundance is frequently observed in stocks of pelagic fishes, and is usually ascribed to fluctuations in oceanographic processes important to survival of pelagic eggs and larvae. Thus one contending explanation for the apparent rise and fall of the armorhead stock is dramatic environment-driven fluctuation in year-class strength.

Another reasonable hypothesis is that trawling effort by Japanese and Soviet vessels during the 1970's reduced the armorhead spawning stock to such low levels that recruitment has been undermined. If this alternative is true, or if fishery-independent factors have driven spawning biomass down to such critical levels, then a restoration of catch and CPUE to higher levels might require a temporary relaxation of fishing effort.

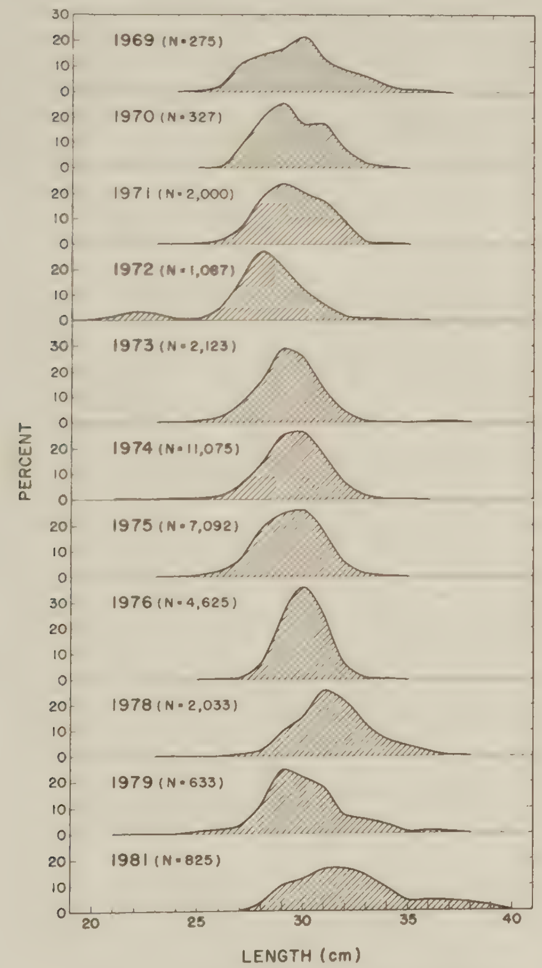

Figure 4.—Percentage frequency distributions of fork length for samples of pelagic armorhead taken by Japanese trawlers on Milwaukee Seamounts.

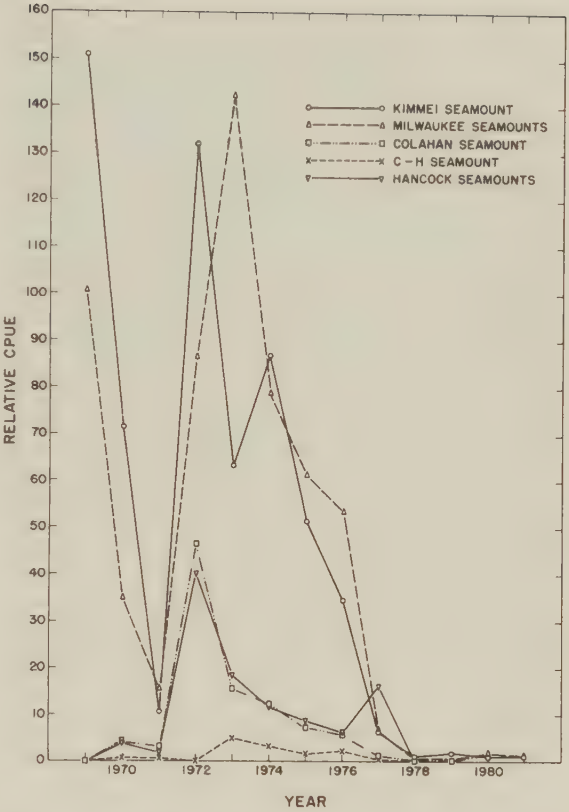

Figure 5.—Annual pelagic armorhead catch per unit of effort (CPUE) for Japanese trawlers on central North Pacific seamounts relative to CPUE in 1981 index period.

ANALYSIS OF STOCK DYNAMICS

To assess the condition of the armorhead stock and evaluate competing hypotheses relating to the impacts of fishing and environmental factors it is useful, if not essential, to construct a quantitative model of the stock dynamics. Using just the Japanese catch and effort statistics, we attempted to construct a model which would account for the observed behavior of the pelagic armorhead fishery and be reasonably consistent with available information and current thinking regarding armorhead life history. In doing so we recognized that our results might be seriously compromised by the absence of data on Soviet catches, and that our sketchy knowledge of armorhead biology would necessitate numerous assumptions.

Biological assumptions

As a basis for the modeling, we made the following assumptions concerning armorhead biology and life history:

1) The armorhead found on the seamounts are derived from a pool of pelagic larvae generated by a common parental spawning biomass. Offspring produced on individual seamounts are distributed widely in the North Pacific and mix thoroughly during their prerecruit stages.

2) Upon reaching sexual maturity at about 2 years of age, armorhead abandon the epipelagic zone inhabited by the juveniles and are recruited to spawning stocks occupying the tops of the seamounts. At the sizes found on the seamounts armorhead are known to be mature, and recent studies at the Honolulu Laboratory on sagittae, vertebral centra, spines, and other hard parts indicate that armorhead 26-32 cm FL are predominantly 2 years of age (J. H. Uchiyama, Southwest Fish. Center Honolulu Lab., unpubl. data). These estimates of age contradict earlier findings by Chikuni (1970), based on scales from two preserved specimens, which assign ages of 3 years to 22 cm fish and 6 years to 32 cm armorhead. Vasil'kov and Borets (1978) also estimated the ages of armorhead. Using a spectral analysis of scale thickness, they suggested that armorhead of 28-33 cm may be as old as 11 years.

3) Over a wide range in abundance of the armorhead spawning stock, the average recruitment is constant. Only at very low spawning stock levels is the average number of recruits stock-dependent. This set of assumptions is consistent with observations on the spawner-recruit relationships in other fishes with pelagic eggs and larvae, such as tunas.

4) The catchability coefficient (the instantaneous fishing mortality inflicted by a unit of trawling effort) may depend on the abundance of armorhead on the seamount. One possibility, for example, is that at low stock densities the catchability coefficient increases. This would be particularly likely if trawlers seek out and target individual schools of armorhead and if reduced armorhead stocks consist of fewer schools.

5) The seamounts are the only spawning ground of the armorhead, so that the CPUE of the trawlers, as some function of the exploitable biomass, provides a measure of the spawning stock.

6) The natural mortality rate of armorhead in the seamount spawning stocks is constant.

7) The temporal changes in armorhead biomass on the Milwaukee Seamounts are representative of trends in the spawning stock as a whole. This assumption seems reasonable enough, although the overall variation in CPUE at Milwaukee is somewhat greater than that at Colahan and Hancock.

8) The fraction of the total annual recruitment which settles out on Milwaukee is constant. Again, this seems generally consistent with the observed patterns of CPUE on the several seamounts.

Autoregressive stock model

With these assumptions, the temporal dynamics of the armorhead spawning stock residing on the seamounts and exploited by the fishery may be approximated by the following simple equation:

$$\underbrace{B_i}_{\substack{\text{Average}\\ \text{spawning}\\ \text{biomass in}\\ \text{period } i}} = \underbrace{W_i}_{\substack{\text{Average}\\ \text{weight of}\\ \text{mature}\\ \text{armorhead}\\ \text{in period } i}} \{\underbrace{N_{i-1}\ S_{i-1,i}}_{\substack{\text{Average}\\ \text{residual}\\ \text{spawning}\\ \text{stock from}\\ \text{period } i\text{-1}}} + \underbrace{R_i\ S_i}_{\substack{\text{Average no.}\\ \text{of recruits}\\ \text{available in}\\ \text{period } i}}\} + \underbrace{\lambda_i}_{\substack{\text{Random}\\ \text{error}\\ \text{term}}}$$

The average armorhead biomass in the *i*-th time period is assumed equal to the average biomass of fish surviving from the previous period, plus the average biomass of those newly recruited during the period, plus a random error term. The explicit dependence of spawning biomass in one period on the same random variable one period prior classifies this model as "autoregressive." Since the average abundance of armorhead during each interval is approximated by the abundance at the midpoint, the survival rate $S_{i-1,i}$ is considered to be a function of the natural mortality rate and trawling effort in periods *i*-1 and *i*, whereas S_i depends only on natural mortality and effort in period *i*. The total number of fish recruited in period *i*, R_i, is assumed to depend on the average armorhead spawning biomass δ time periods earlier. In particular, we assumed the following functions for the survival rates and recruitment:

$$S_{i-1,i} = e^{-\{M + [H(N_{i-1})\ E_{i-1} + \mathrm{H}(N_i)\ E_i]/2\}}$$

$$S_i = e^{-\{M + H(N_i)\ E_i\}/2}$$

and

$$R_i = \alpha \left\{1 - e^{-\beta N_{i-\delta}\ W_{i-\delta}}\right\} \varepsilon_i$$

Here α is the average recruitment expected at the highest levels of spawning biomass, and β determines the rate at which average recruitment declines as spawning stock is reduced. The term ε_i is a lognormal random "disturbance" representing the unexplained variability in recruitment.

In the survival functions, the natural mortality coefficient is denoted by M, and the nominal trawling effort in period *i* by E_i. The catchability coefficient in period *i*, $H(N_i)$ is written as a function of average stock size during the period, N_i. In particular, we considered the power function

$$H(N_i) = Q\ N_i^{\gamma}$$

now commonly used in models of schooling fish harvested contagiously. In many such cases it has been found that $\gamma < 0$, i.e., catchability is inversely related to average stock size. When $\gamma = 0$, catchability is constant.

The average individual weights in each year, W_i, were estimated from Japanese length-frequency statistics and a length-weight relationship computed from NMFS data. The resulting series of average weights was then smoothed before use in the model.

The random error term ε_i is assumed to have a mean of 1, but a variance which may depend on *i* and/or the spawning biomass in period *i*. Further, the ε_i are probably serially correlated. The distributions of the ε_i may also reflect oceanographic processes affecting the survival of armorhead eggs and larvae or the settlement of mature armorhead onto the seamounts. The sequence of error terms λ_i is assumed to have zero mean and a dispersion matrix which depends on a host of factors, including stochastic variation in recruitment, autocorrelation in the series of spawning biomass estimates, and random variation in the mortality processes.

To estimate parameters of the armorhead stock model we made the usual assumption that stock density was measured by some function of CPUE. In our case the appropriate function is

$$N_i = \left\{\frac{\mathrm{CPUE}_i}{W_i\ Q}\right\}^{\frac{1}{\gamma+1}}$$

The complete nonlinear regression model is given in the Appendix.

Estimation procedures

Since there were five parameters to estimate (α, β, γ, Q, M), a long time series of observations was required. Neither annual nor semiannual data would provide sufficient degrees of freedom. Therefore the model was fit to monthly CPUE and effort data. A problem arose here because monthly CPUE time series were not complete, yet lagged spawning biomass estimates were needed for each time period. Instead of circumventing the problem by aggregating the monthly data we developed an iterative EM algorithm (see Dempster et al. 1977) which simultaneously predicted the values of missing observations and computed weighted least squares estimates of the model parameters.

Visual analysis of the Milwaukee Seamounts time series

Because the only suitably complete monthly CPUE time series was for Milwaukee Seamounts, we used those data exclusively for the trial fitting. Restriction of the analysis to Milwaukee Seamounts necessitated assumptions 7 and 8 above. Before attempting to fit the regression model with the EM algorithm, we inspected the monthly time series of CPUE and nominal trawling effort at Milwaukee and the annual CPUE series at all seamounts to see if the model was compatible with the data, to extract initial estimates for the model parameters and to see if we could anticipate any problems in the fitting. A byproduct of this cursory inspection was a preliminary evaluation of the impact of Japanese trawling on the armorhead stock.

The monthly CPUE for Milwaukee is shown in Figure 6, beginning in September 1969 and continuing for 146 months through October 1981. Neglecting the first 4 months, when only 12 h of trawling were done by Japanese vessels, we considered the series beginning in January 1970. In general the monthly data show a considerable amount of variation, but reliability of the CPUE statistics, measured by the corresponding trawling effort, also varies greatly. If the model is correct, declines in average CPUE from month to month are due to an excess of mortality over recruitment, and increases in CPUE reflect the reverse. Without actually fitting the model, it can be seen that the monthly time series of CPUE and Japanese effort (and their annual and semiannual counterparts; see Figs. 1, 3, and 7) are consistent with the proposed model from 1974 through 1981. That is, the general downward trend of CPUE during this period could have resulted from a recruitment which was directly dependent on spawning stock coupled with a catchability inversely related to stock size. But when examined in its entirety the situation appears more complex. Note that the comparatively high recruitments at all seamounts in 1973 were generated from relatively low spawning biomasses 2 years earlier whereas the peak spawning biomasses in 1972 led to relatively weak year-classes, suggesting either stock-independent recruitment or a dome-shaped stock recruitment relationship (e.g., a Ricker model). The latter alternative does not seem appropriate for armorhead. (The Soviet data also suggest that stock-independent recruitment fluctuations were large during the early 1970's; spawning stocks were apparently

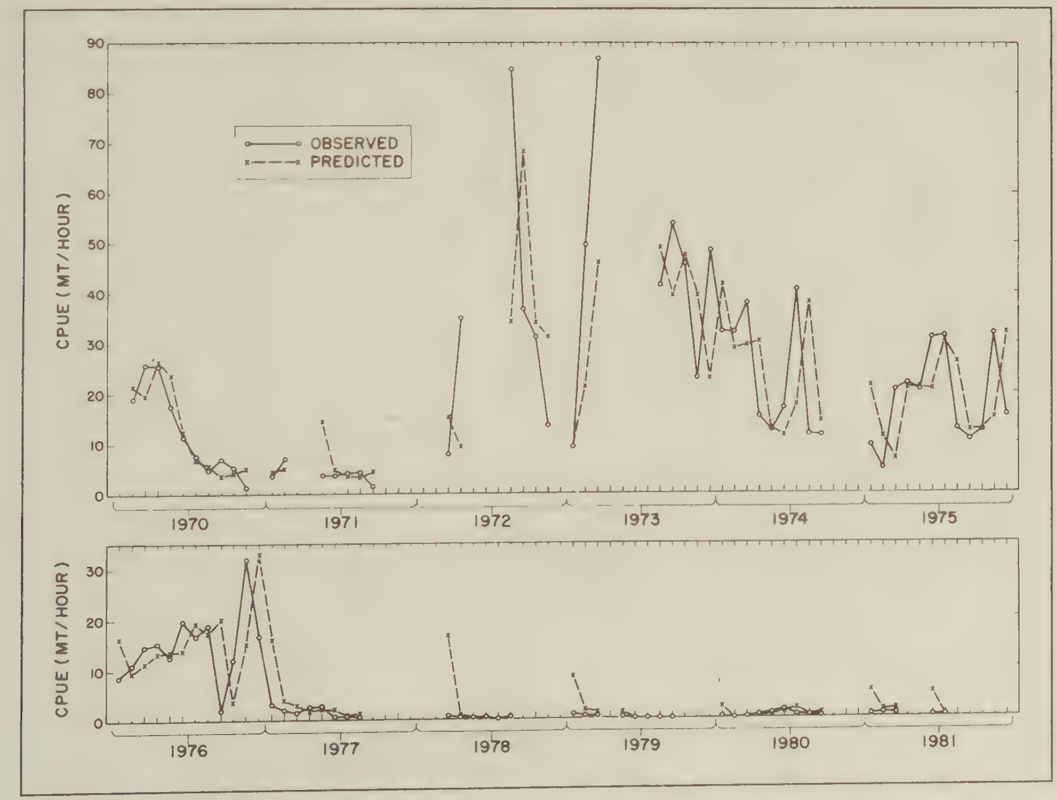

Figure 6.—Observed monthly pelagic armorhead catch per unit of effort (CPUE) by Japanese trawlers on Milwaukee Seamounts and predicted CPUE based on autoregressive model with Ricker spawner-recruit relationship.

about the same size in 1970 and 1973, but resulting recruitments in 1972 and 1975 differed by a factor of 2.5.)

Further analysis yields additional evidence of stock-independent recruitment. For example, relatively modest spawning stocks in 1970 and 1971 (measured by Japanese CPUE) apparently produced large recruitments in 1972 and 1973, whereas spawning stocks of approximately the same size in 1975 and 1976 were unproductive. (This conclusion would be weakened if Japanese trawler catchability increased between 1971 and 1972.) Although the Japanese trawling effort at some seamounts, such as Milwaukee and Kimmei, was substantially greater during the latter period, the difference in fishing intensity could not account for such disparities in the ratios of spawning biomass. (This argument considers only Japanese effort; if a complete record of Soviet effort statistics were available, the conclusion might differ.) Thus it is reasonable to suggest that stock-independent recruitment is the norm for armorhead, except at very low stock levels. The difficult problems are to determine what the critical level is, whether the spawning stock is now below this level and whether a curtailment of fishing would be effective in reversing the trend.

Trial fitting of the model

When the stock model was fit to the monthly Milwaukee time series, only a very poor fit could be obtained. The residuals suggested that the proposed flat-topped stock recruitment relationship was inconsistent with the data. In another attempt a dome-shaped Ricker stock-recruitment model accounted for about 77% of the variation in CPUE (Fig. 6). These results are consistent with the conclusions reached by simple visual inspection of the Japanese CPUE and effort time series. However, despite numerous attempts at fitting the model, stable convergence to a unique set of parameter estimates could not be achieved. Some of the problems in fitting the model are statistical. Consistent and efficient estimation of parameters in models with autocorrelated errors and lagged dependent variables requires that the complex covariance structure of the errors be correctly specified. In our case, it would be necessary to derive the structure analytically and estimate the resulting covariance matrix iteratively as a step in the EM algorithm. Some theoretical work along these lines has been done by Domowitz (1982) for situations involving complete time series, and has been applied to estimation of anchovy stock models.

Further work needs to be done to develop an iteratively reweighted estimation procedure which accounts for the error covariance structure. In our fitting of the model we used statistical weights equal to the nominal effort, assuming this at least provided a measure of the reliability of the spawning biomass indices.

Another problem is that the model is very likely misspecified, particularly regarding recruitment. Our analysis suggests to us that the greatest part of annual variation in recruitment is determined by "random" factors independent of spawning stock, i.e., the term ε_i is of overriding importance. In our simplistic model of recruitment we made use of the only relevant information available, that relating to biomass of the parent stock. However, improved prediction of recruitment might be possible with ancillary data on oceanographic processes, i.e., it might be possible to model ε_i. Two types of processes would likely be important; those that affect survival of armorhead eggs and larvae, and those that influence the congregation of armorhead in the seamount spawning habitat.

Perhaps the most critical problem with the analysis of the Japanese CPUE series is, of course, that only Japanese effort statistics were available. If fishing mortality is an important determinant of stock size, it will be essential to include effort data (or total catch data) from Soviet trawlers. These data will have to be detailed and comprehensive, so that a time series of monthly effort can be constructed for the duration of the fishery.

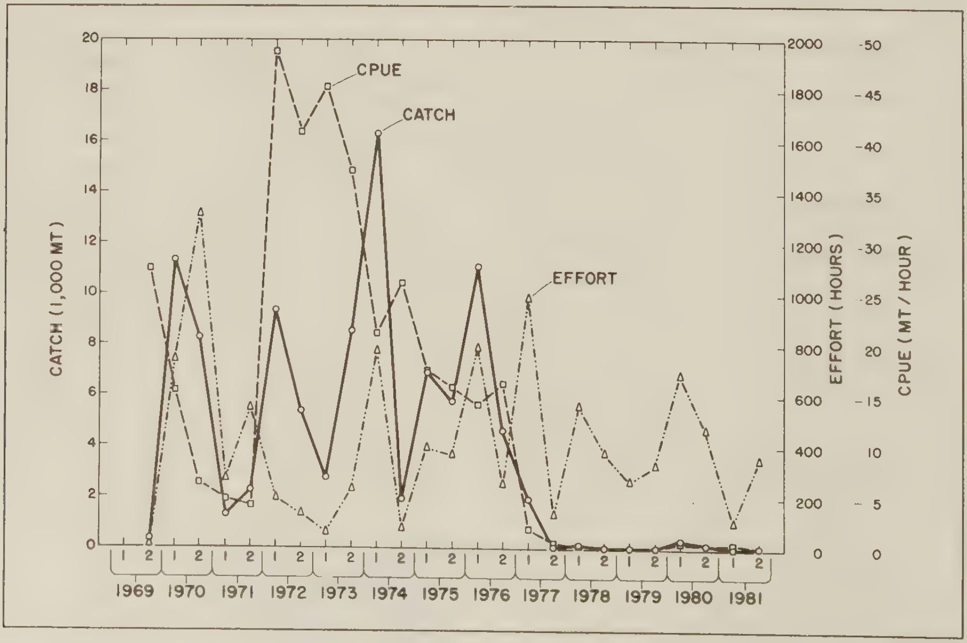

Figure 7.—Semiannual pelagic armorhead catch, effort, and catch per unit of effort (CPUE) for Japanese trawlers on Milwaukee Seamounts.

DIRECTIONS FOR FURTHER RESEARCH

Fish stock assessment is a fairly chancy business under the best of circumstances. It is particularly difficult for armorhead, where we are handicapped by an incomplete record of exploitation and a meager knowledge of basic biology and life history. At this stage our model of stock dynamics consists largely of assumptions, and little in the way of empirical facts. However, we take some comfort in the adage of Box (1979), who noted that "All models are wrong, but some may be useful." We believe our modeling exercise has been helpful, particularly in establishing a context for further investigations of the armorhead stock. Acquisition of more complete fishery statistics and additional biological and hydrographic studies will permit refinements and adjustments.

Several shortcomings of the armorhead stock assessment have been noted, suggesting avenues for further research. The foremost need obviously is to acquire a comprehensive record of the Soviet catch and effort, and repeat the analysis with the full set of fishery statistics. Until then it will not be possible to evaluate the impact of fishing on the armorhead stock.

In addition, we suggest that information on oceanographic processes be examined for clues to the variation in armorhead recruitment. Experience with other species suggests that this will be a difficult task, but worth the effort. Information concerning thermal structure and the behavior of currents in the region of the Emperor-Hawaiian Ridge seems to be in fair abundance, and it would be useful to attempt even rough models of the habitat of armorhead during their critical early stages and the environmental conditions affecting recruitment of adults to the seamounts. One specific objective would be to seek an explanation for the sudden collapse of the armorhead spawning biomass in 1978, and the apparent rise of alfonsin. A starting point may be the finding of Mizuno and White (1983), based on analysis of TRANSPAC XBT casts and IODC data from long. 130°E to 170°W that the Kuroshio meander weakened substantially beginning in 1978 or 1979, accompanied by a southward displacement of the Kuroshio Extension by 2° to lat. 34°N. Associated with this was increased instability in the meander and a doubling of eddy formation.

Other work needs to be done to establish the age distribution and the growth rates of armorhead. We assumed that the spawning stock consisted primarily of fish 2 years of age, so that the CPUE statistics not only provided a measure of spawning biomass in year *i* but also gave information on the recruitment produced by the parent stock in year *i*-2. If the larger armorhead on the seamounts are much older, say 5 or 6 years or more, different conclusions might be reached.

Our modeling made no specific mention of the striking morphological variation which has been noted in armorhead. As described by Humphreys and Tagami (1986), immature "fat-type" armorhead are characteristically found in the epipelagic waters of the northeastern Pacific, whereas mature "lean-type" fish occupy the seamounts. One reasonable hypothesis is that the fat-type armorhead are storing energy which is then expended later in reproduction. An important question for population dynamics and ecosystem energetics therefore is, "how long is the reproductive phase?" The autoregressive model simply subtracts mortality and adds recruitment from one period to the next, and makes no assumptions about the number of age groups in the spawning stock. However, if the age estimates by the Honolulu Laboratory are accurate, we are tempted to suggest that armorhead have a short life once they mature and recruit to the seamounts. Such an hypothesis is consistent with the predominance of lean-type armorhead in the spawning stock, and with the occurrence of emaciated, spent fish in the catches. Thus in some respects the life cycle of armorhead may resemble that of salmon or squid, and similar models of the population dynamics may be applicable.

Table 1.—Pelagic armorhead, *Pentaceros richardsoni*, catch (metric tons), effort (hours of trawling), and catch per unit effort (CPUE) (metric tons/hour) by Japanese stern trawlers on the central North Pacific seamounts.

Year/ Month	Catch	Effort	CPUE
Kimmei Seamount			
1969			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	106	28	3.79
Sept.	648	55	11.78
Oct.	2,203	64	34.42
Nov.	2,140	60	35.67
Dec.	1,983	91	21.79
1970			
Jan.	2,485	146	17.02
Feb.	709	24	29.54
Mar.	0	0	—
Apr.	533	68	7.84
May	760	82	9.27
June	20	6	3.33
July	72	9	8.00
Aug	496	109	4 55
Sept.	0	0	—
Oct.	63	14	4.50
Nov.	0	0	—
Dec.	0	0	—
1971			
Jan.	7	7	1.00
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	88	28	3.14
June	0	0	—
July	0	0	—
Aug.	0	23	0.00
Sept.	0	0	—
Oct.	0	0	-
Nov.	0	0	—
Dec.	0	0	
1972			
Jan.	0	0	—
Feb.	5	11	0.45
Mar.	0	0	—
Apr.	72	1	72.0
May	0	0	—
June	0	0	–
July	0	0	-
Aug.	0	0	—
Sept.	0	0	-
Oct.	0	0	—
Nov.	768	51	15.06
Dec.	1,170	34	34.41
1973			
Jan.	376	38	9.89
Feb.	148	22	6.73
Mar.	0	0	—
Apr.	0	0	–
May	0	0	-
June	0	0	-
July	0	0	-
Aug.	0	0	—
Sept.	149	6	24.83
Oct.	52	4	13.00
Nov	124	10	12.40
Dec.	45	10	4.50
1974			
Jan.	0	0	—
Feb.	124	2	62.00
Mar.	88	6	14.67
Apr.	152	16	9.50
May	397	52	7.63
June	108	12	9.00
July	812	73	11.12
Aug	1,561	92	16.97
Sept.	773	41	18.85
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1975			
Jan.	0	18	0.00
Feb	1,071	93	11.52
Mar.	543	56	9.70
Apr.	96	25	3 84
May	0	0	—
June	0	0	—
July	31	11	2.82
Aug.	201	14	14.36
Sept.	877	142	6.18
Oct.	374	44	8.50
Nov.	168	30	5.60
Dec.	429	37	11.59
1976			
Jan.	2	1	2.00
Feb.	206	46	4.48
Mar.	69	10	6.90
Apr.	17	1	17.00
May	1,822	408	4 47
June	1,743	255	6.84
July	606	115	5.27
Aug.	754	181	4 17
Sept.	950	149	6.38
Oct.	50	20	2.50
Nov.	168	30	5.60
Dec.	429	37	11.59
1977			
Jan.	0	0	–
Feb.	155	87	1.78
Mar.	734	773	0.95
Apr.	143	202	0.71
May	160	127	1.26
June	9	30	0.30
July	6	14	0.43
Aug.	0	0	
Sept.	0	0	—
Oct.	0	0	
Nov.	0	0	—
Dec.	0	0	—
1978			
Jan.	0	0	–
Feb.	0	0	—
Mar.	0	0	—
Apr.	132	226	0.58
May	17	312	0.05
June	22	347	0.06
July	6	152	0.04
Aug	3	83	0.04
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec	0	0	-
1979			
Jan.	76	121	0.63
Feb.	88	189	0.47
Mar.	24	89	0.27
Apr.	1	15	0.07
May	6	66	0.09
June	1	29	0.03
July	1	58	0.02
Aug.	0	112	0.00
Sept.	2	51	0.04
Oct.	0	0	-
Nov.	0	0	-
Dec.	0	0	
1980			
Jan.	1	26	0.04
Feb.	18	141	0.13
Mar.	35	166	0.21
Apr.	10	74	0.14
May	7	32	0.22
June	1	21	0.05
July	1	6	0.17
Aug.	0	5	0.00
Sept.	0	6	0.00
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	
1981			
Jan	0	4	0.00
Feb.	37	27	1.37
Mar.	12	127	0.09
Apr.	0	0	—
May	0	0	—
June	10	89	0.11
July	13	67	0.19
Aug.	3	32	0.09
Sept.	13	126	0.10
Oct.	1	94	0.01
Milwaukee Seamounts			
1969			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	0	0	—
Sept	323	10	32.30
Oct.	0	0	
Nov.	7	2	3.50
Dec.	0	0	—
1970			
Jan.	544	26	20.92
Feb	1,692	89	19.01
Mar.	1,188	46	25 83
Apr.	821	32	25.66
May	2,619	150	17.46
June	4,481	396	11.32
July	2,495	322	7.75
Aug.	1,073	222	4.83
Sept.	2,794	402	6.95
Oct.	1,885	361	5.22
Nov.	8	6	1.33
Dec.	0	0	—
Milwaukee Seamounts (*cont.*)			
1971			
Jan.	68	19	3.58
Feb.	600	86	6.98
Mar.	0	0	—
Apr	0	0	—
May	171	46	3.72
June	436	119	3 66
July	989	239	4 14
Aug.	1,213	284	4 27
Sept.	38	25	1.52
Oct	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1972			
Jan.	0	0	—
Feb	0	0	—
Mar.	643	82	7.84
Apr.	2,722	78	34 90
May	6,103	34	179 50
June	0	0	—
July	0	0	—
Aug.	1,693	20	84.65
Sept.	2,120	58	36.55
Oct.	1,465	47	31 17
Nov.	81	6	13.50
Dec.	0	1	0.00
1973			
Jan.	459	24	19.13
Feb.	1,140	23	49.57
Mar.	1,129	13	86.85
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	785	19	41.32
Sept.	1,714	32	53 56
Oct.	2,146	47	45.66
Nov.	2,208	97	22 76
Dec.	1,691	35	48.31
1974			
Jan.	3,375	105	32.14
Feb.	2,911	91	31.99
Mar.	2,683	71	37 79
Apr.	2,957	194	15 24
May	2,434	196	12.42
June	1,979	117	16.91
July	1,498	37	40.49
Aug.	339	29	11 69
Sept.	92	8	11 50
Oct.	0	0	-
Nov	0	0	—
Dec.	0	0	-
1975			
Jan	838	86	9.74
Feb.	199	40	4.98
Mar.	1,044	51	20.47
Apr.	1,748	80	21 85
May	2,209	108	20 45
June	870	28	31 07
July	1,594	51	31 25
Aug.	2,358	186	12.68
Sept	782	75	10 43
Oct.	259	21	12 33
Nov.	540	17	31 76
Dec.	246	16	15 38

Table 1.—*Continued.*

Year/ Month	Catch	Effort	CPUE
1976			
Jan.	883	103	8.57
Feb.	1,058	97	10.91
Mar.	2,070	141	14.68
Apr.	4,389	288	15.24
May	787	63	12.49
June	1,910	97	19.69
July	1,716	104	16.50
Aug.	1,178	63	18.70
Sept.	50	26	1.92
Oct.	299	25	11.96
Nov.	540	17	31.76
Dec.	278	17	16.35
1977			
Jan.	428	139	3.08
Feb.	122	65	1.88
Mar.	85	65	1.31
Apr.	540	226	2.39
May	617	237	2.60
June	156	254	0.61
July	69	114	0.61
Aug.	8	19	0.42
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1978			
Jan.	0	0	—
Feb.	0	0	—
Mar.	22	45	0.49
Apr.	45	133	0.34
May	29	191	0.15
June	38	192	0.20
July	38	335	0.11
Aug.	11	41	0.27
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1979			
Jan.	11	13	0.85
Feb.	11	25	0.44
Mar.	9	31	0.29
Apr.	0	0	—
May	11	108	0.10
June	9	85	0.11
July	13	89	0.15
Aug.	9	92	0.10
Sept.	14	144	0.10
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1980			
Jan.	25	113	0.22
Feb.	11	102	0.11
Mar.	31	131	0.24
Apr.	59	157	0.38
May	61	78	0.78
June	173	104	1.66
July	54	150	0.36
Aug.	84	195	0.43
Sept.	38	120	0.32
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1981			
Jan	3	6	0.50
Feb.	30	43	0.70
Mar.	12	18	0.67
Apr.	0	0	—
May	0	0	—
June	8	36	0.22
July	34	112	0.30
Aug.	29	178	0.16
Sept.	8	59	0.14
Oct.	0	2	0.00
Colahan Seamount			
1970			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	206	57	3.61
June	466	42	11.10
July	202	23	8.78
Aug.	3	2	1.50
Sept.	0	0	—
Oct.	39	4	9.75
Nov.	0	0	—
Dec.	0	0	—
1971			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	367	58	6.33
June	339	59	5.75
July	0	0	—
Aug.	0	0	—
Sept.	482	96	5.02
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1972			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	6,552	32	204.75
July	3,815	52	73.37
Aug.	1,212	15	80.80
Sept.	1,265	34	37.21
Oct.	0	0	—
Nov.	700	24	29.17
Dec.	621	14	44.36
1973			
Jan.	169	23	7.35
Feb.	108	2	54.00
Mar.	563	13	43.31
Apr.	791	9	87.89
May	0	0	—
June	644	28	23.00
July	0	0	—
Aug.	482	14	34.43
Sept.	240	16	15.00
Oct.	132	3	44.00
Nov.	1,058	40	26.45
Dec.	732	28	26.14
Colahan Seamount (*cont.*)			
1974			
Jan.	142	9	15.78
Feb.	407	12	33.92
Mar.	255	5	51.00
Apr.	300	15	20.00
May	0	0	—
June	95	11	8.64
July	0	0	—
Aug.	137	7	19.57
Sept.	71	6	11.83
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1975			
Jan.	202	12	16.83
Feb.	143	23	6.22
Mar.	0	0	—
Apr.	148	11	13.45
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	143	14	10.21
Sept.	394	34	11.59
Oct.	175	13	13.46
Nov.	483	22	21.95
Dec.	102	11	9.27
1976			
Jan.	130	21	6.19
Feb.	41	7	5.86
Mar.	23	8	2.88
Apr.	0	0	—
May	50	4	12.50
June	213	8	26.63
July	0	3	0.00
Aug.	0	4	0.00
Sept.	169	24	7.04
Oct.	117	18	6.50
Nov.	483	22	21.95
Dec.	102	11	9.27
1977			
Jan	6	1	6.00
Feb.	33	18	1.83
Mar.	0	0	—
Apr.	5	8	0.63
May	29	7	4.14
June	1	1	1.00
July	0	0	—
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1978			
Jan.	0	0	—
Feb.	0	0	—
Mar.	16	32	0.50
Apr.	37	51	0.73
May	27	10	2.70
June	8	30	0.27
July	1	13	0.08
Aug.	2	12	0.17
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1979			
Jan.	28	22	1.27
Feb.	0	4	0.00
Mar.	0	0	—
Apr.	0	0	—
May	4	29	0.14
June	20	25	0.80
July	15	28	0.54
Aug.	6	12	0.50
Sept.	2	9	0.22
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1980			
Jan.	1	7	0.14
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	244	48	5.08
June	41	18	2.28
July	96	26	3.69
Aug.	39	54	0.72
Sept.	12	27	0.44
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1981			
Jan.	116	10	11.60
Feb.	55	22	2.50
Mar.	16	9	1.78
Apr.	0	0	—
May	0	0	—
June	6	20	0.30
July	4	32	0.13
Aug.	2	8	0.25
Sept.	9	12	0.75
Oct.	0	4	0.00
C-H Seamount			
1970			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	91	5	18.20
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	102	21	4.86
Dec.	0	0	—
1971			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	130	23	5.65
June	212	26	8.15
July	0	0	—
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—

Table 1.—*Continued.*

Year/ Month	Catch	Effort	CPUE
C-H Seamount (*cont.*)			
1973			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	81	3	27.00
July	0	0	—
Aug.	469	6	78.17
Sept.	536	9	59.56
Oct.	252	4	63.00
Nov.	701	14	50.07
Dec.	492	9	54.67
1974			
Jan.	0	0	—
Feb.	283	8	35.38
Mar.	154	3	51.33
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	251	8	31.38
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1975			
Jan.	123	4	30.75
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	62	2	31.00
Sept.	453	35	12.94
Oct.	0	0	—
Nov.	72	1	72.00
Dec.	52	4	13.00
1976			
Jan.	63	2	31.50
Feb.	25	3	8.33
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	0	0	—
Sept.	0	0	—
Oct	176	6	29.33
Nov.	72	1	72.00
Dec.	52	4	13.00
1977			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	10	6	1.67
May	12	3	4.00
June	1	4	0.25
July	0	0	—
Aug.	0	0	—
Sept.	0	0	—
Oct	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1978			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	3	5	0.60
June	1	13	0.08
July	0	0	—
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1979			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	2	3	0.67
July	2	2	1.00
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1980			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	37	6	6.17
June	4	1	4.00
July	1	5	0.20
Aug.	13	10	1.30
Sept.	8	8	1.00
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1981			
Jan.	51	5	10.20
Feb.	99	7	14.14
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	2	1	2.00
July	0	0	—
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Hancock Seamounts			
1970			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	41	7	5.86
June	15	2	7.50
July	34	4	8.50
Aug.	90	4	22.50
Sept.	0	0	—
Oct.	0	0	—
Nov.	140	28	5.00
Dec.	0	0	—
Hancock Seamounts (*cont.*)			
1971			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	81	23	3.52
June	0	0	—
July	0	0	—
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1972			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	1,870	24	77.92
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	783	13	60.23
Dec.	705	8	88.13
1973			
Jan.	1,320	26	50.77
Feb.	614	5	122.80
Mar.	886	15	59.07
Apr.	0	0	—
May	0	0	—
June	593	12	49.42
July	2,296	75	30.61
Aug.	843	51	16.53
Sept.	340	7	48.57
Oct.	138	3	46.00
Nov.	581	30	19.37
Dec.	393	15	26.20
1974			
Jan.	205	11	18.64
Feb.	0	0	—
Mar.	219	3	73.00
Apr.	75	6	12.50
May	14	1	14.00
June	72	4	18.00
July	0	0	—
Aug.	0	0	—
Sept.	39	4	9.75
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1975			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	169	17	9.94
Sept.	265	14	18.93
Oct.	218	12	18.17
Nov.	404	19	21.26
Dec.	265	19	13.95
1976			
Jan.	112	22	5.09
Feb.	47	4	11.75
Mar.	24	4	6.00
Apr.	0	0	—
May	0	0	—
June	163	21	7.76
July	0	0	—
Aug.	0	0	—
Sept.	30	4	7.50
Oct.	67	8	8.38
Nov.	404	16	25.25
Dec.	265	19	13.95
1977			
Jan.	53	10	5.30
Feb.	17	19	0.89
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1978			
Jan.	0	0	
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	178	6	29.67
June	0	0	—
July	0	0	—
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1979			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	23	10	2.30
June	39	61	0.64
July	5	22	0.23
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1980			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	42	11	3.82
Sept.	189	102	1.85
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—

Table 1.—*Continued.*

Year/ Month	Catch	Effort	CPUE
1981			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	234	46	5.09
July	0	0	—
Aug.	39	61	0.64
Sept.	130	114	1.14
Oct.	0	0	—
Others			
1970			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	95	25	3.80
Dec.	0	0	—
1971			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	6	6	1.00
June	319	61	5.23
July	0	0	—
Aug.	0	4	0.00
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1972			
Jan.	0	0	—
Feb.	5	2	2.50
Mar.	29	5	5.80
Apr.	0	0	—
May	0	0	—
June	25	1	25.00
July	0	0	—
Aug.	123	2	61.50
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	117	1	117.00
1973			
Jan.	21	13	1.62
Feb.	2	14	0.14
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	167	6	27.83
July	169	6	28.17
Aug.	15	3	5.00
Sept.	0	0	—
Oct.	138	1	138.00
Nov.	187	12	15.58
Dec.	42	1	42.00

Year/ Month	Catch	Effort	CPUE
Others (*cont.*)			
1974			
Jan.	0	0	—
Feb.	64	1	64.00
Mar.	571	6	95.17
Apr.	23	2	11.50
May	57	1	57.00
June	83	8	10.38
July	235	7	33.57
Aug.	0	0	—
Sept.	72	4	18.00
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1975			
Jan.	0	5	0.00
Feb.	0	0	—
Mar.	0	0	—
Apr.	63	3	21.00
May	0	0	—
June	151	5	30.20
July	0	0	—
Aug.	774	35	22.11
Sept.	184	5	36.80
Oct.	241	12	20.08
Nov.	0	0	—
Dec.	32	1	32.00
1976			
Jan.	97	16	6.06
Feb.	39	2	19.50
Mar.	34	7	4.86
Apr.	0	0	—
May	132	28	4.71
June	245	29	8.45
July	71	11	6.46
Aug.	181	15	12.07
Sept.	141	19	7.42
Oct.	59	4	14.75
Nov.	0	3	0.00
Dec.	0	0	—
1977			
Jan.	0	0	—
Feb.	13	9	1.44
Mar.	0	6	0.00
Apr.	8	8	1.00
May	26	6	4.33
June	6	7	0.86
July	0	0	—
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1978			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	12	27	0.44
May	231	38	6.08
June	1	13	0.08
July	0	21	0.00
Aug.	0	5	0.00
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—

Year/ Month	Catch	Effort	CPUE
1979			
Jan.	0	0	—
Feb.	0	2	0.00
Mar.	0	0	—
Apr.	0	0	—
May	11	17	0.65
June	43	96	0.45
July	14	48	0.29
Aug.	0	0	—
Sept.	0	0	—
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1980			
Jan.	0	0	—
Feb.	2	5	0.40
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	293	71	4.13
Sept.	212	155	1.37
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1981			
Jan.	0	0	—
Feb.	22	8	2.75
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	150	33	4.55
July	12	34	0.35
Aug.	12	58	0.21
Sept.	38	126	0.30
Oct.	1	1	1.00
Total			
1969			
Jan.	0	0	—
Feb.	0	0	—
Mar.	0	0	—
Apr.	0	0	—
May	0	0	—
June	0	0	—
July	0	0	—
Aug.	106	28	3.79
Sept.	971	65	14.94
Oct.	2,203	64	34.42
Nov.	2,147	62	34.63
Dec.	1,983	91	21.79
1970			
Jan.	3,029	172	17.61
Feb.	2,401	113	21.25
Mar.	1,188	46	25.83
Apr.	1,354	100	13.54
May	3,626	296	12.25
June	4,982	446	11.17
July	2,894	363	7.97
Aug.	1,662	337	4.93
Sept.	2,794	402	6.95
Oct.	1,987	379	5.24
Nov.	345	80	4.31
Dec.	0	0	—

Year/ Month	Catch	Effort	CPUE
Total (*cont.*)			
1971			
Jan.	75	26	2.89
Feb.	600	86	6.98
Mar.	0	0	—
Apr.	0	0	—
May	843	184	4.58
June	1,306	265	4.93
July	989	239	4.14
Aug.	1,213	311	3.90
Sept.	520	121	4.30
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1972			
Jan.	0	0	—
Feb.	10	13	0.77
Mar.	672	87	7.72
Apr.	2,794	79	35.37
May	6,103	34	179.50
June	6,577	33	199.30
July	5,685	76	74.80
Aug.	3,028	37	81.84
Sept.	3,385	92	36.79
Oct.	1,465	47	31.17
Nov.	2,332	94	24.81
Dec.	2,613	58	45.05
1973			
Jan.	2,345	124	18.91
Feb.	2,012	66	30.49
Mar.	2,578	41	62.88
Apr.	791	9	87.89
May	0	0	—
June	1,485	49	30.31
July	2,465	81	30.43
Aug.	2,594	93	27.89
Sept.	2,979	70	42.56
Oct.	2,858	62	46.10
Nov.	4,859	203	23.94
Dec.	3,395	98	34.64
1974			
Jan.	3,722	125	29.78
Feb.	3,789	114	33.24
Mar.	3,970	94	42.23
Apr.	3,507	233	15.05
May	2,902	250	11.61
June	2,337	152	15.38
July	2,545	117	21.75
Aug.	2,288	136	16.82
Sept.	1,047	63	16.62
Oct.	0	0	—
Nov.	0	0	—
Dec.	0	0	—
1975			
Jan.	1,163	125	9.30
Feb.	1,413	156	9.06
Mar.	1,587	107	14.83
Apr.	2,055	119	17.27
May	2,209	108	20.45
June	1,021	33	30.94
July	1,625	62	26.21
Aug.	3,707	268	13.83
Sept.	2,955	305	9.69
Oct.	1,267	102	12.42
Nov.	1,667	89	18.73
Dec.	1,126	88	12.80

Table 1.—*Continued.*

Year/ Month	Catch	Effort	CPUE	Year/ Month	Catch	Effort	CPUE
Total *(cont.)*							
1976				1979			
Jan.	1,287	165	7.80	Jan.	115	156	0.74
Feb.	1,416	159	8.91	Feb.	99	220	0.45
Mar.	2,220	170	13.06	Mar.	33	120	0.28
Apr.	4,406	289	15.25	Apr.	1	15	0.07
May	2,791	503	5.55	May	55	230	0.24
June	4,274	410	10.42	June	114	299	0.38
July	2,393	233	10.27	July	50	247	0.20
Aug.	2,113	263	8.03	Aug.	15	216	0.07
Sept.	1,340	222	6.04	Sept.	18	204	0.09
Oct.	768	81	9.48	Oct.	0	0	—
Nov.	1,667	89	18.73	Nov.	0	0	—
Dec.	1,126	88	12.80	Dec.	0	0	—
1977				1980			
Jan.	487	150	3.25	Jan.	27	146	0.18
Feb.	340	198	1.72	Feb.	31	248	0.13
Mar.	819	844	0.97	Mar.	66	297	0.22
Apr.	706	450	1.57	Apr.	69	231	0.30
May	844	380	2.22	May	349	164	2.13
June	173	296	0.58	June	219	144	1.52
July	75	128	0.59	July	152	187	0.81
Aug.	8	19	0.42	Aug.	471	346	1.36
Sept.	0	0	—	Sept.	459	418	1.10
Oct.	0	0	—	Oct.	0	0	—
Nov.	0	0	—	Nov.	0	0	—
Dec.	0	0	—	Dec.	0	0	—
1978				1981			
Jan.	0	0	—	Jan.	170	25	6.80
Feb.	0	0	—	Feb.	243	107	2.27
Mar.	38	77	0.49	Mar.	40	154	0.26
Apr.	226	437	0.52	Apr.	0	0	—
May	485	562	0.86	May	0	0	—
June	70	595	0.12	June	410	225	1.82
July	45	521	0.09	July	63	245	0.26
Aug.	16	141	0.11	Aug.	85	337	0.25
Sept.	0	0	—	Sept.	198	437	0.45
Oct.	0	0	—	Oct.	2	101	0.02
Nov.	0	0	—				
Dec.	0	0	—				

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Appendix

Parameters of the autoregressive stock model

Parameters of the autoregressive stock model were estimated iteratively by minimizing the weighted sum of squares

$$\Phi = \sum_{i=1}^{n} E_i\,[\mathrm{CPUE}_i - \widehat{\mathrm{CPUE}}_i]^2$$

where n = total number of data points in the time series. The squared residuals were weighted by effort, E_i, so that time periods with no observation of CPUE (i.e., $E_i = 0$) did not contribute to Φ and had no bearing on the parameter estimation.

Predicted CPUE's for every time period (including those with zero effort) were computed at each iteration by

$$\widehat{\mathrm{CPUE}}_i = \left\{ \left(\frac{W_i}{W_{i-1}} \right)^a \mathrm{CPUE}^a_{i-1}\, S_{i-1,i} + R_i\, Q^a\, W_i^a\, S_i \right\}^{\frac{1}{a}}$$

where

$$S_{i-1,i} = \mathrm{e}^{-(M+F_{i-1,i})}$$

$$S_i = \mathrm{e}^{-(M+F_i)/2}$$

$$R_i = \alpha \left[1 - \mathrm{e}^{-\beta P_{i\text{-}\delta}} \right]$$

and the auxilliary variables are defined as

$$F_{i-1,i} = Q^a \left[\left(\frac{\mathrm{CPUE}_{i-1}}{W_{i-1}} \right)^b E_{i-1} + \left(\frac{\mathrm{CPUE}_i}{W_i} \right)^b E_i \right] /2$$

$$F_i = Q^a \left(\frac{\mathrm{CPUE}_i}{W_i} \right)^b E_i$$

$$P_{i-\delta} = W^b_{i-\delta} \left(\frac{\mathrm{CPUE}_{i-\delta}}{Q} \right)^a$$

$$a = 1/(\gamma + 1)$$

$$b = \gamma/(\gamma + 1).$$

Lagged spawning biomasses for the first δ time periods in the observed series were assumed equal to the spawning biomass in period 1.

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THE RELATIVE MAGNITUDE OF THE 1985 PACIFIC SARDINE SPAWNING BIOMASS OFF SOUTHERN CALIFORNIA

PATRICIA WOLF
California Department of Fish and Game
245 West Broadway
Long Beach, California 90802

PAUL E. SMITH
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

ABSTRACT

The spawning biomass of the Pacific sardine off southern California during 1985 is considered to be at least 20,000 short tons[1]. This determination was made using an inverse egg production or "egg production area" method, which estimates the area over which a specified spawning biomass (20,000 tons) would be expected to occur. Our survey had a 95% probability of detecting the spawning area within the survey area if at least 20,000 tons of adults were present. This method was developed from the egg production method, which estimates adult biomass from measurements of egg production in the spawning area and from the egg production rate of the adult population. Using estimates of the components of egg production and specific fecundity for sardines from previous studies, we predicted that 20,000 tons of spawning biomass would cover a spawning area of about 500 n.mi^2.

A total of 86 sardine eggs was collected at 11 of 419 stations during the May 1985 survey, which ranged from San Diego to Point Conception and extended from within one mile of the coast to approximately 80 miles offshore. Spawning occurred mainly along the Santa Barbara Ventura coast and covered an estimated 670 n.mi^2. A total of 1,170 anchovy eggs and 266 anchovy larvae were found at 114 and 69 of the stations, respectively.

As provided by state law when the sardine biomass reaches 20,000 tons, a 1,000-ton fishery for sardines was opened on January 1, 1986. This is the first directed fishery allowed for California sardines since a moratorium on sardine fishing was enacted in 1974. Adult reproductive parameters and egg survival must be determined for absolute biomass estimation.

RESUMEN

La biomasa de desove de la sardina del Pacifico frente al Sur de California fue estimada en por lo menos 20,000 toneladas cortas (1 tonelada corta = 0.907 toneladas métricas) en 1985. Esta determinación fue hecha por medio del método inverso de producción de huevos o "área de producción de huevos." Este método estima el área en la cual una biomasa de desove dada (20,000 toneladas) supuestamente tendrá lugar. Nuestro estudio permitiría localizar el área de desove dentro del área de estudio con un 95% de probabilidad si hubieran, al menos, 20,000 toneladas de adultos. Este método está basado en el método de producción de huevos el cual evalúa la biomasa de adultos a partir de medidas de la producción de huevos en el área de desove, y de la tasa de producción de huevos por la población de adultos. Sobre la base de estudios previos sobre la producción de huevos y la fecundidad específica de las sardinas, se pronostican 20,000 toneladas de biomasa de desove en un área de desove de alrededor de 500 mi.n^2.

Se colectaron 86 huevos de sardinas en 11 de 419 estaciones ubicadas entre San Diego y Point Conception, y que se extendían entre 1 y aproximadamente 80 millas mar afuera, durante mayo de 1985. El desove ocurrió a lo largo de la costa entre Santa Barbara y Ventura principalmente, cubriendo un área estimada en 670 mi.n^2. Se encontraron 1,170 huevos y 266 larvas de anchoveta en 114 y 69 de las estaciones, respectivamente.

De acuerdo con la legislación estatal, cuando la biomasa de sardina alcanzó 20,000 toneladas, se abrió una pesquería para 1,000 toneladas de este recurso el 1° de enero de 1986. Esta es la primera pesquería dirigida que se permite para las sardinas de California desde la implementación, en 1974, de una veda de esta pesquería. Para obtener una estimación absoluta de la biomasa, los parámetros reproductivos de los adultos y la sobrevivencia de los huevos deben ser determinados.

INTRODUCTION

This report assesses the 1985 spawning biomass of the Pacific sardine. Legislation closing the sardine fishery in 1974 requires the Department of Fish and Game to determine annually whether the spawning biomass is more than 20,000 tons. This legislation imposes a moratorium on fishing sardines while the biomass remains below 20,000 tons and allows a 1,000-

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[1] Commercial landings, tonnages specified in legislation, and tonnages in this paper are reported in short tons

ton fishery when the biomass exceeds this level. Earlier assessments of the sardine spawning biomass were based on ichthyoplankton surveys, aerial observations, trawl surveys, and incidental landings in mackerel and live bait fisheries, and have shown signs of increase since 1980 (Wolf 1985; Klingbeil and Wolf 1984; Klingbeil 1981, 1982, 1983).

Because the sardine population appeared to increase, a quantitative method for detecting recovery and determining whether the biomass had exceeded 20,000 tons was required. Estimates of the sardine population biomass during the fishery were based on analysis of catch and age data (Murphy 1966; MacCall 1979). The egg production method (Parker 1980) is currently used to estimate spawning biomass of anchovies off California (Picquelle and Hewitt 1983) and anchovies and sardines off Peru (Santander et al. 1982). However, available methods of biomass estimation are not applicable at low biomass levels; the cost and effort necessary to achieve meaningful levels of precision are too high.

We developed the egg production area method to allow a cost-efficient, quantitative determination of the relative magnitude of spawning biomass while levels remain low. Details of the method and survey design are described by Wolf and Smith (1985). Here we apply the egg production area method to assess the relative magnitude of the sardine spawning biomass during 1985.

EGG PRODUCTION METHOD

The egg production method estimates spawning biomass as

$$B = P_o A \frac{kw}{RFS}$$

where B = spawning biomass (MT)
P_o = daily egg production, number of eggs produced per 0.05 m^2 of sea-surface area,
W = average weight of mature females (g),
R = sex ratio, fraction of population that is female, by weight (g),
F = batch fecundity, number of eggs spawned per mature female per batch,
S = fraction of mature females spawning per day,
A = total area of survey (0.05 m^2), and
k = conversion factor from grams to metric tons.

This method was derived by Parker (1980), and applied by Picquelle and Hewitt (1983, 1984) and Hewitt (1985) to estimate northern anchovy biomass.

EGG PRODUCTION AREA METHOD

In the egg production method, daily egg production and population fecundity parameters are measured during the survey. An exponential mortality model is fit to counts of aged eggs, and P_o is estimated by extrapolating back to the number of eggs at the time of spawning. Parameters W, F, S, and R are estimated from samples of adult fish collected during the survey.

In the egg production area method, the spawning biomass is specified and the equation solved for A_1:

$$A_1 = \frac{B_1 \, R \, F \, S \, m}{P_o \, k_1 \, W}$$

where A_1 = spawning area of biomass B_1 in nautical miles^2.
B_1 = spawning biomass, in short tons,
k_1 = conversion factor from grams to tons,
m = conversion factor from 0.05 m^2 to nautical miles^2.

The procedure for estimating sardine spawning area differs from that used for anchovy[2] in that occasional stations with no eggs are incorporated for anchovy: a slight increase in area is compensated by a slight decrease in mean abundance of eggs. For the sardine spawning area estimate, only stations with eggs are included. We assumed that an area represented by a single sample is not entirely covered, but that this is compensated by the fact that eggs might be present in another area represented by a sample containing no eggs.

We used information from previous studies to estimate the parameters, P_o, W, F, S, and R for sardines rather than collecting measurements during the survey. These values (Table 1) are not known or have not been measured recently for California sardines; we adapted existing information concerning sardines and related species (Wolf and Smith 1985).

Estimates of daily egg production for sardines and anchovies off Peru[3] indicate that egg production rates are lower for sardines than for anchovies by a factor of 1:2. We applied this relationship to annual estimates from 1980 through 1984 (Hewitt 1985) of daily egg production rates for anchovies (approximately 10 eggs/0.05 m^2) to obtain an estimate of sardine daily egg production of about 5 eggs/0.05 m^2. Historical CalCOFI egg surveys yielded an estimated California sardine daily egg production rate of approximately 1.5 eggs/0.05 m^2. This value is thought to be low, however, be-

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[2] Lasker, R. (ed.) MS. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*)

[3] Smith, P.E., H. Santander, and J. Alheit. MS. Comparison of the mortality and dispersal of sardine (*Sardinops sagax sagax*) and anchovy (*Engraulis ringens*) eggs off Peru.

TABLE 1
Parameters Used to Estimate Spawning Area, and Resulting Estimates

B_1	W	R	F	P_o	S	A_1
Spawning biomass (short tons)	Average female weight (g)	Sex ratio (females/total)	Batch fecundity (eggs batch/ female)	Egg production (eggs/.05m^2-day)	Spawning fraction (spawning females/ total females)	Spawning area (nautical miles^2)
20.000	120	0.5	32.000	5.0	0.02	141
					0.05	353
					0.10	706
					0.15	1.058
				1.5	0.02	470
					0.05	1.176
					0.10	2.352
					0.15	3.528

cause the sampling technique (oblique tows instead of vertical tows) may have overestimated the surface area of water sampled. Both values of P_o were used (Table 1). Average weight of mature females, W, was estimated to be 120 grams, and batch fecundity, F, was estimated at 32,000 eggs (MacGregor 1957). The female fraction of the population by weight, R, was assumed to be half. Spawning fraction, S, for other pelagic species ranges from 0.02 females spawning per day (spawning once every 50 days) for Pacific sauries (Hatanaka 1956) to 0.14 females spawning per day (spawning once every 7 days) for anchovies (Hunter and Macewicz 1980). Spawning fraction for sardines off Peru (J. Alheit, Instituto del Mar del Perú, pers. comm.) and for sardines off the west coast of Baja California (J.R. Torres-Villegas, CICIMAR, unpublished data) has been estimated at about 0.06 females spawning per day. The range values of S was used (Table 1).

The calculated area, A_1, over which 20,000 tons of Pacific sardines could be expected to spawn ranges from 141 to 1,058 n.mi.^{2}, for an estimated daily egg production rate of 5 eggs/0.05 m^2 and an estimated range of values for spawning fraction, and from 470 to 3,525 n.mi.^{2} for a daily egg production rate of 1.5 eggs/ 0.05 m^2 and the same range of values for spawning fraction (Table 1). With available information, we consider the higher value of P_o—5.0 eggs/0.05 m^2—and a value of S ranging between 0.05 and 0.10 females spawning per day to be the best estimates of these parameters for sardines. Therefore, 500 n.mi.^{2} was selected as a useful estimate of A_1.

SURVEY DESIGN

The survey area and time of year over which sardine spawning would be likely to occur were determined from occurrences of sardine eggs and larvae in historical CalCOFI survey data (Wolf and Smith 1985). The critical spawning area, A_1, estimated at 500 n.mi.^{2}, was approximately 2% of the survey area, which included CalCOFI regions 7 and 8 and covered an estimated 32.000 n.mi.^{2} (Smith et al. 1976). Using a table for determining confidence limits of a proportion (Natrella 1963), we determined the number of stations (374) representing the minimum effort required to locate the spawning area within the survey area, with a high probability (95%) of detecting the spawning area if 20.000 tons of spawning adults were actually present. The stations were spaced 4 n.mi. apart offshore and 10 n.mi. apart alongshore according to standard anchovy egg production procedures. Because each station represents 40 n.mi.^{2}, the calculated spawning area that 20.000 tons of sardines would cover was expected to contain 12 or 13 positive stations.

SURVEY DESCRIPTION

The survey was conducted by NOAA ship *David Starr Jordan* from April 29 through May 19, 1985. Stations were occupied from south to north, beginning at San Diego and ending at Point Sal, and extending offshore an average distance of about 80 miles (Figure 1). Plankton samples were collected at 419 stations using a 25-cm-diameter CalVET (vertical egg tow) net of 150-micron mesh that was retrieved vertically from 70 m (when depth allowed) to the surface. Samples were collected at all hours. No stations were occupied in established shipping lanes.

Sardine and anchovy eggs and larvae were identified, sorted, and counted. A total of 86 sardine eggs occurred at 11 stations, with the number of eggs per station ranging from 1 to 42 (Figure 2). Most of the positive stations occurred along the coast near Santa Barbara, and in the eastern portion of the Santa Barbara Channel, from Port Hueneme to Anacapa and Santa Cruz islands. Two positive stations occurred off Newport Beach. Sardine larvae occurred at 10 stations, in approximately the same areas as eggs. Eggs and larvae in combination occurred at 16 stations.

Evidence of anchovy spawning (1,710 eggs and 266

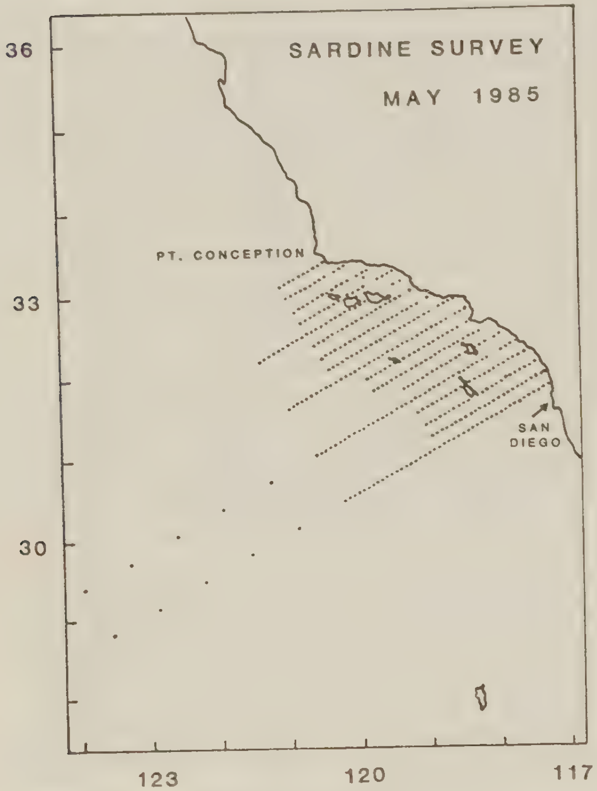

Figure 1. Stations occupied during sardine survey, May 1985.

larvae at 114 and 69 stations, respectively) was considerably more common but occurred in different areas than sardine spawning. Anchovy eggs and larvae were concentrated mostly in the southern portion of the survey near San Diego.

Two of the samples had to be discarded because of inadequate preservation. Neither were adjacent to or near stations at which sardine eggs occurred (Figure 2).

SPAWNING AREA

Spawning area was determined by multiplying the number of egg-positive stations by the area represented by each station (40 n.mi.^{2}). Some stations that were positive for sardine eggs were adjacent to areas that were not sampled, either because the area occurred in the shipping lanes or was close to shore and aligned in such a way that the station plan did not call for a sample. In order to consider these areas in the spawning area estimate, we adjusted the area of positive stations adjacent to an unsampled area to include half of the adjacent unsampled area, averaged along lines in order of station occupation and estimated by eye. The area of positive stations too near to shore to include an entire 40 n.mi.^{2} were also adjusted to reflect the portion of the 4 by 10 n.mi.^{2} actually sampled.

An unadjusted estimate of the spawning area equals 440 n. mi^2. An estimate of the spawning area adjusted as described above is 670 n.mi.^{2} (Figure 2). Both of these estimates are within the range of spawning area calculated for 20,000 tons of spawning biomass of sardines and are close to the selected estimate of A_1 (Table 1).

DISCUSSION

The egg production area method allows detection of the onset of sardine recovery and provides an objective, quantitative technique for determining the relative magnitude of spawning biomass. This is particularly useful when the management plan requires determining whether a specified spawning biomass level has been exceeded, but either the level to be ascertained remains low enough that developing a direct estimate with reasonable precision is cost- and effort-prohibitive, or information beyond the relative magnitude of biomass is unnecessary.

Because the spawning area observed during the survey was close to that predicted for 20,000 tons of adult sardines, the spawning biomass of sardines off California is considered to be at least 20,000 tons in 1985. As specified by state law, this determination allowed the initiation of a 1,000-ton fishery in January 1986. The provision for a fishery was included in the 1974 moratorium legislation because of concern that a total moratorium would preclude detecting the onset of recovery. Also, simulations of a 5% fishery at that biomass level projected no deleterious effects (W. Lenarz, NMFS, Tiburon, pers. comm.). MacCall's (1979) estimates of apparently lower recruitment rates at low biomass levels suggest that Lenarz's projections may be optimistic.

The large range of values calculated for A_1 resulted from using a range of values to estimate parameters P_o (daily egg production rate) and S (spawning fraction). These parameters are not known for Pacific sardines. Two other parameters—W (average female weight) and F (batch fecundity)—were estimated from sardines taken from the 1945-46 commercial catch. The average monthly mean weight of mature female sardines occurring incidentally with mackerel during 1985 was 142 grams. As discussed below, all of the components of egg production and specific fecundity are dynamic and have been shown to vary from year to year for northern anchovy (Hewitt 1985). Daily egg production rate and spawning fraction must be determined for Pacific sardines; the adult parameters should be obtained simultaneously. The egg production area method, however, uses historical information.

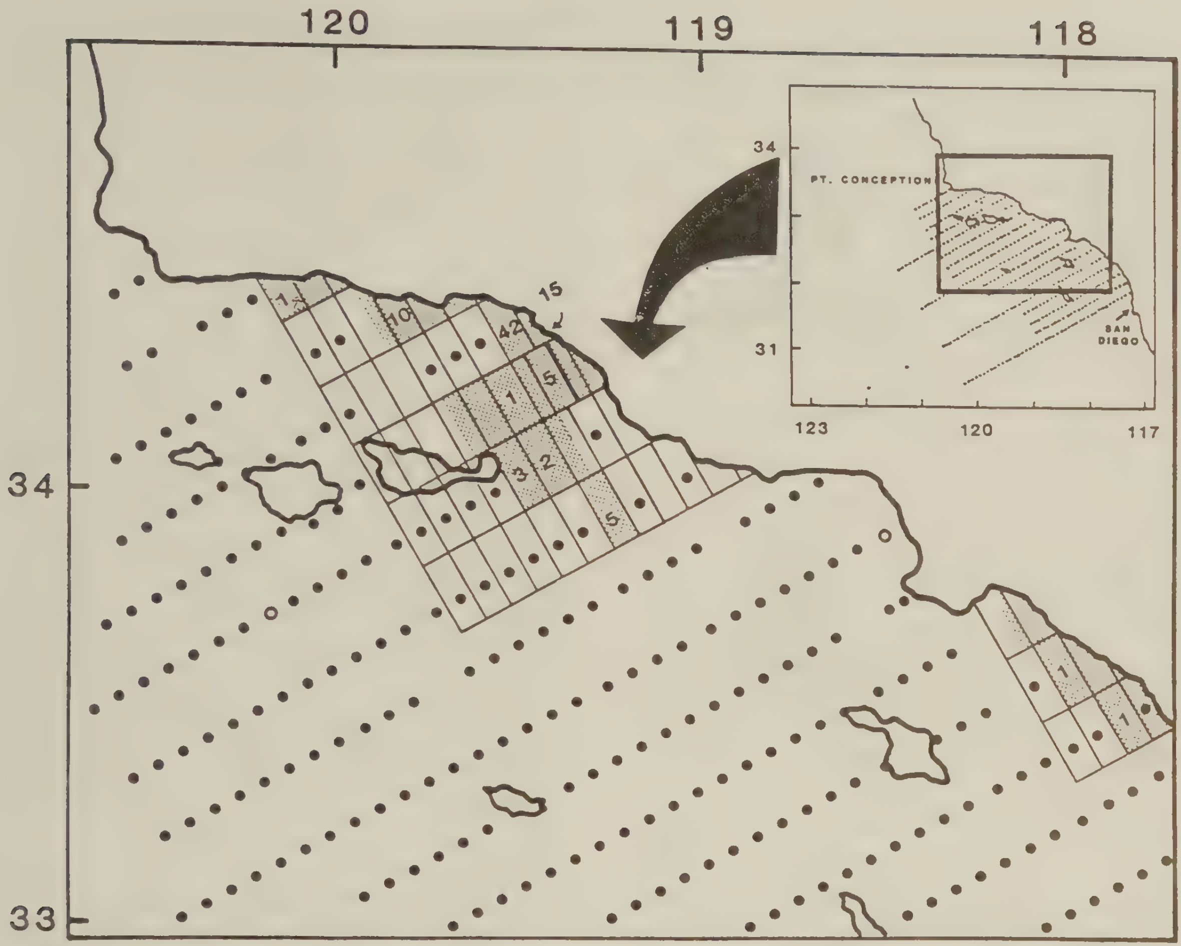

Figure 2. Number of eggs per station and location of stations that contained sardine eggs. Rectangles outline 4-by-10-n.mi.^{2} areas represented by each station to illustrate spawning area adjustment. Shaded area is adjusted sardine spawning area. Open circles are discarded samples.

Several other sources provide additional information concerning the status of the adult Pacific sardine population during 1985. Incidental landings of sardines with mackerel during 1985 totalled 652 tons, the largest annual take in 20 years ("Review of Some California Fisheries for 1985," this volume). Sardines have become increasingly more common in mackerel landings, occurring in 50% of observed landings in 1985 compared to 30% in 1984. Catch length frequencies of incidental sardines show a trend from 1983 through 1985 of a broader length distribution, indicating recruitment in 1985 (Figure 3). Sardines from the 1985 year class were detected in early 1966 in Monterey Bay, indicating that spawning occurred north of Point Conception and beyond the range of the survey. Sardines ranked first in biomass and third in abundance in purse seine hauls from Long Beach Harbor during 1983 and the first half of 1984 (C. Mitchell, MBC Applied Environmental Sciences, pers. comm.). No detectable trend, however, was observed in the mean number of sardines captured by purse seine off San Onofre from 1983 through 1985 (E. DeMartini, UCSB Fish Program, pers. comm.).

The abundance of sardine eggs and larvae in four nearshore ichthyoplankton transects in the Southern California Bight increased two to three orders of magnitude from 1978-79 through 1982-84, and sardines ranked third in overall abundance during that period (R.J. Lavenberg, Los Angeles County Natural History Museum, pers. comm.). From 1978 through 1984, monthly mean numbers of sardine larvae in coastal waters near San Onofre increased steadily (W. Watson, Marine Ecological Consultants of Southern California, pers. comm.). Both of these studies indicate that a sub-

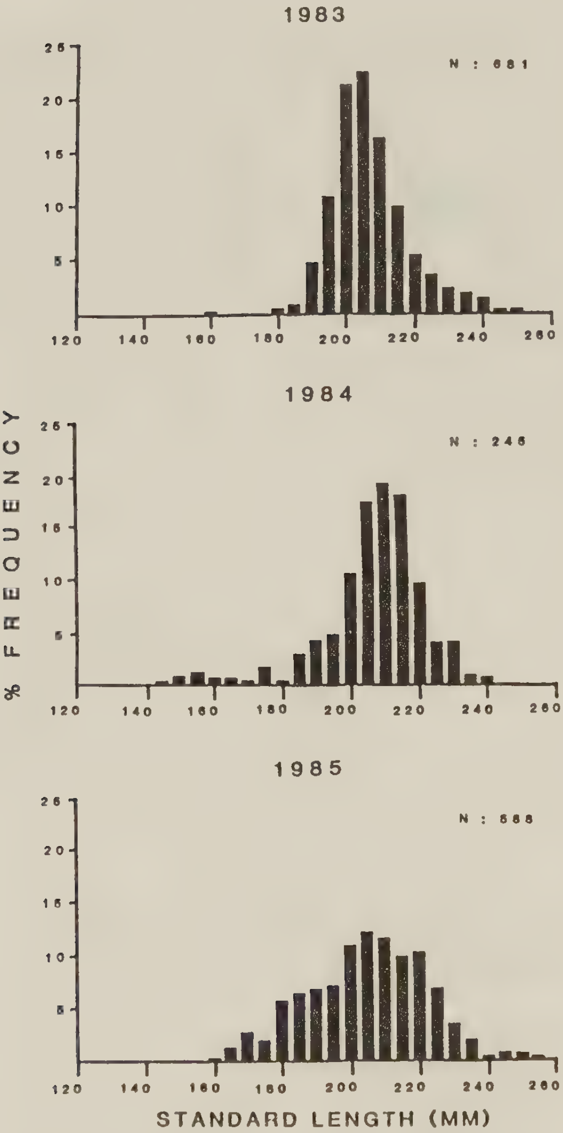

Figure 3. Catch length frequencies of sardines landed incidentally with mackerel in 1983, 1984, and 1985. Mean weights of modal length classes for each year are: 1983, 130 g, 205-209 mm SL; 1984, 147 g, 210-214 mm SL; 1985, 143 g, 205-209 mm SL.

stantial portion of sardine spawning in recent years has occurred relatively near to shore (within the 75-m contour) and during summer and fall.

Although the limited interpretation of the 1985 survey is conclusive in the original objectives relative to 20,000-ton spawning biomass, we resist broadening these few results for a biomass estimate or fishery quota. The spawning area of 670 n.mi.^{2} is nearly identical to the 500 n.mi.^{2} criterion adopted for this technique. This means that any deviation from the assumed adult parameters could change the evaluation. Another critical feature is that we can estimate only the standing crop of eggs from this small set, not the egg production. The two unevaluated factors are mortality rate of the eggs and the precision of the intercept estimate. Future surveys must quantify the mortality rate and the frequency distribution of eggs.

The estimated mean of positive samples in the 1985 survey is high relative to samples of the 1930s to 1950s (Table 2). It appears that the high value is due to the chance encounter of more observations with high values. We believe the cause of this difference is technical rather than biological, although this cannot be determined from these few samples. It is important to note that all the other distributions result from oblique or horizontal tows and that the new results are from a vertical tow. The scale of the integration is 25 cm for the CalVET net and on the order of meters for all but one of the other nets, and kilometers for the high-speed net used in 1950. The smaller CalVET net will have a greater probability of sampling zero eggs. Also, the sampling threshold of the CalVET net (1 egg in a CalVET is equivalent to 50 eggs in a 1-m oblique tow) might cause the lower end of the frequency distribution of egg densities to be undersampled. Both of these characteristics would cause the mean observed density of positive samples to be inflated. This would imply that the entire area of sardine spawning was not detected and that 20,000 tons is a conservative estimate.

The high mean value could also result from a lower than normal mortality or higher than normal per capita egg production rate, which would imply a lower spawning biomass. These biological factors will all have to be separately assessed for the absolute biomass to be estimated from egg production rates.

Analogous data from the anchovy egg production procedure indicate the great importance of the adult sampling effort for biomass estimation. If the interval between batches of eggs is long, for example 20 days, the ratio of gonads with evidence of spawning in the previous day is only 5%. This ratio would require many independent samples to precisely determine the spawning fraction. Individual samples of anchovy females range from 0% spawning to over 40% when the mean is 15%. Thus the overall precision of spawning biomass estimates may be determined by the ability to obtain a sufficient number of independent samples of adult females.

In summary, at least one more year of field and laboratory work on additional egg samples and adult collections will be required before the procedure for an absolute biomass estimate can be designed.

TABLE 2
Pacific Sardine Egg Sample Frequency Distributions at Different Levels of Spawning Biomass[a]

#/10 m^2		Net types and years					
x	ln (x)	CalVET 1985	CF&G 2-m 1931-32	1-m 1941	0.5-m 1941	Hi-speed 1950	1-m 1959
.125	−2.08	—[b]	2	—	—	—	—
.5	−0.69	—	4	—	—	—	—
2	0.69	—	6	21	—	—	28
8	2.08	—	7	22	8	—	28
32	3.47	—	14	16	15	—	30
128	4.85	4	12	31	29	77	23
512	6.24	4	13	27	14	20	12
2,048	7.62	2	5	17	10	7	5
8,192	9.01	1	2	3	2	1	4
Estimated mean		1,564	544	569	619	406	410
Biomass (MT)[c]		0.02	3.9	2.7	2.7	1.0	0.2

[a](Smith and Richardson 1977)
[b]Value below sampler threshold
[c](Murphy 1966)

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Sexual dimorphism in four species of rockfish genus *Sebastes* (Scorpaenidae)

Tina Wyllie Echeverria
Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920, U.S.A.

Keywords: Morphology, Sexual selection, Natural selection, Parental care, Discriminant analysis

Synopsis

Sexual dimorphisms, and factors influencing the evolution of these differences, have been investigated for four species of rockfish: *Sebastes melanops, S. flavidus, S. mystinus,* and *S. serranoides.* These four species, which have similar ecology, tend to aggregate by species with males and females staying together throughout the year. In all four species adult females reach larger sizes than males, which probably relates to their role in reproduction. The number of eggs produced increases with size, so that natural selection has favored larger females. It appears males were subjected to different selective pressures than females. It was more advantageous for males to mature quickly, to become reproductive, than to expend energy on growth. Other sexually dimorphic features include larger eyes in males of all four species and longer pectoral fin rays in males of the three piscivorous species: *S. melanops, S. flavidus,* and *S. serranoides.* The larger pectoral fins may permit smaller males to coexist with females by increasing acceleration and, together with the proportionately larger eye, enable the male to compete successfully with the female to capture elusive prey (the latter not necessarily useful for the planktivore *S. mystinus*). Since the size of the eye is equivalent in both sexes of the same age, visual perception should be comparable for both sexes.

Introduction

Natural selection is a mechanism of evolution which can influence physical characteristics of a species, characteristics which reflect selective pressures in the species environment. Sexual selection is a component of natural selection that acts independently upon males or females. Sexual dimorphism can result from either component.

Sexual dimorphisms, which occur in every major group of vertebrates, are commonly manifested in mammals as size differences, in birds as color variations, in reptiles as defensive structures, and in amphibians as sounds. Fishes of both fresh and salt water also exhibit sexual dimorphisms: in swordtails (*Xiphophorus* sp.) and gobies (*Gobius* sp.) as fin variations, in guppies (*Poecilia* sp.) and wrasses (*Labrus* sp.) as color variations, in eels (*Anguilla* sp.) and mullets (*Mugil* sp.) as size differences, and in silurids (*Ompok* sp.) (Rao & Karamchandani 1971) and sculpins (*Myoxocephalus* sp.) as morphological variations in body proportions (Breder & Rosen 1966).

In fishes, secondary sexual dimorphisms are often associated with species that have internal fertilization or protection of the eggs or young by a parent (Breder & Rosen 1966). Despite the widespread relationship between internal fertilization and secondary sexual dimorphism, one of the most speciose groups of live bearers in the northeast

Pacific Ocean, the rockfishes (*Sebastes*) with approximately 70 species occurring in that region, does not show obvious sexual dimorphisms.

Four species of *Sebastes* were studied: *S. melanops*, the black rockfish; *S. flavidus*, the yellowtail rockfish; *S. mystinus*, the blue rockfish; and *S. serranoides*, the olive rockfish. All four species are very similar in body shape and size, with convex interorbital spaces, weak head spines and a dusky olive-to-black coloration, all key characters used in the identification of rockfish (Miller & Lea 1976). Similarities include morphologies and reproductive characteristics while they are separated ecologically by different diets, feeding times, and depth distributions. These four species have been studied more than other rockfish because they comprise a large part of the commercial and sport-fishing landings, and are readily accessible in large aggregations near shore.

In *Sebastes* the contribution to the survival of young is primarily accomplished by the female. Fertilization is internal with possible storage of sperm by the female (Sorokin 1967). During gestation the arterial supply to the gonad serves for the exchange of metabolic wastes (Moser 1967) and the ovarian fluid provides some nutrition for the developing embroys (Boehlert & Yoklavich 1984). Fecundity varies among species, but is always large, increasing with the size of the female (Phillips 1964, Boehlert et al. 1982), with some species possibly having two broods per year (Moser 1967, MacGregor 1970). In *Sebastes*, selection has favored increasing reproductive success by means of large females capable of producing and accommodating large numbers of embryos.

The only reports of morphological differences between sexes of *Sebastes* are provided by Chen (1971) and Moser (1967). Chen found sexual dimorphism in *Sebastes umbrosus*, with males having a shorter pre-anal length but a greater anal base, upper jaw length, anal ray length, snout length and prepelvic length ($P<0.01$). Moser noted differences in the urogenital papilla of *Sebastodes paucispinis*. In this investigation body measurements taken from four species of rockfish have been analyzed to determine (1) if Chen's findings are more widespread, (2) if there are morphological differences between the sexes of any one species that could be used, in themselves, to characterize the sexes, and (3) if there are differences, what their significance might be.

Working within the definitions of selection that have been made here, an attempt will be made to discern which component – natural or sexual selection – may have exerted the greater influence in any sexually dimorphic feature found in these four species of *Sebastes*. Natural selection will be credited for those features that primarily affect the survival of the entire species, while sexual selection will be limited to those features that affect the reproductive advantage of one individual over another.

Methods

Rockfish were collected throughout 1977 from three localities along the coast of central California; Point Reyes, the Farallon Islands, and Cordell Bank (Fig. 1). These localities lie at the corners of a triangle covering roughly 250 square miles. This relatively limited area was chosen because Miller & Geibel (1973) showed that growth rates in blue rockfish from widely separated geographic areas differed. Fish used in the morphometric study were collected as part of a survey of age and length in the rockfishes of central California (Sen 1984), and constitute a subsample of the fish used in that survey.

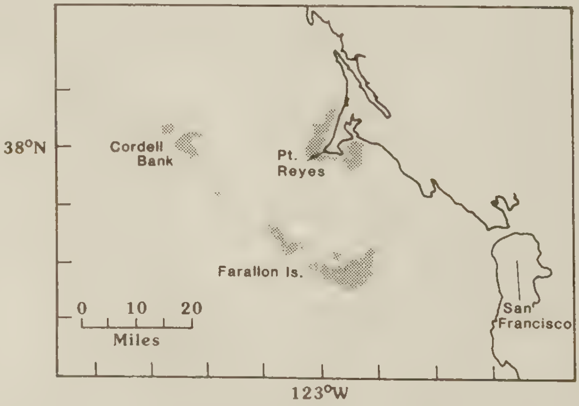

Fig. 1. Rockfish in this study were collected from Pt. Reyes, the Farallon Is. and Cordell Bank where the depth was <40 fathoms.

Specimens were collected from the hook-and-line sportfishing fleet. Fish were filleted on board the fishing boat, and the carcasses were collected and handled in a standardized way to reduce the variability in measurements which occurs between whole fish and carcasses or fresh and frozen fish (Forrester 1967). In the laboratory the otoliths (Sagitta) were collected, the gonad state was determined, and 23 body parts, in addition to standard length, were measured.

Ages of the four species were determined by counting one opaque and one translucent zone of the otolith. Annular growth increments were validated up to 12 years in the black rockfish by Six & Horton (1977), up to 12 years in the yellowtail rockfish by Kimura et al. (1979), and up to 4 years in the olive rockfish by Love & Westphal (1981). Ages of blue rockfish have been determined from scale annuli and comparison between the growth zones of the otoliths and scales showed similiar patterns (Miller & Geibel 1973). All researchers agreed that, for the ages studied, one opaque and one translucent zone are deposited per year. Fish collected in this study also included individuals older than those from previous studies and it was assumed the reliability of the annual marks continued beyond the ages obtained in previous studies.

The average length of the males and females at each age was used to compare growth rates between the sexes. The comparisons were made from all fish sampled (Table 1).

Sex and the stage of gonadal development were determined in the laboratory. Sexes were identified by gonadal inspection: ovaries were characterized by an egg mass encased by the ovarian wall while the testis were characterized by appearing solid in cross-section. Ovaries were classified as: immature, with developing eggs, eggs containing eyed embryos or spent. Testis were classified as: immature, undergoing spermatogenesis, or spent. Gonad states of specimens collected throughout the year were used to determine the reproductive seasonality.

Morphometric measurements were made with vernier calipers (±0.01 mm) on freshly thawed fish carcasses. The 24 body parts measured included: total length, fork length, standard length, head length, length of the base of the anal fin, snout length, interorbital width, width of the orbit, length of the upper jaw, lower jaw projection, width of the pectoral fin base, longest pectoral fin

Table 1. Mean standard length (mm) at age for males (M) and females (F) in four species of rockfish collected during 1977. Numbers (N) of individuals used to calculate length in parentheses.

Age (yr)	*S. melanops*				*S. flavidus*				*S. mystinus*				*S. serranoides*			
	M	(N)	F	(N)	M	(N)	F	(N)	M	(N)	F	(N)	M	(N)	F	(N)
4			283	(4)	235	(4)	227	(8)	189	(3)						
5	288	(3)	294	(7)	259	(8)	259	(13)	229	(9)	234	(4)	258	(3)	283	(1)
6	326	(18)	320	(22)	282	(5)	282	(3)	233	(10)	267	(19)	294	(21)	304	(3)
7	352	(25)	336	(14)	300	(11)	303	(10)	256	(11)	270	(20)	313	(12)	338	(13)
8	377	(21)	383	(10)	309	(15)	326	(18)	265	(11)	294	(15)	321	(13)	339	(13)
9	383	(22)	395	(18)	323	(17)	330	(16)	268	(13)	302	(15)	336	(3)	365	(9)
10	388	(20)	402	(10)	331	(21)	340	(23)	275	(12)	315	(14)	349	(3)	389	(11)
11	405	(14)	423	(4)	339	(35)	357	(26)			323	(11)			417	(7)
12	401	(7)	420	(4)	352	(28)	361	(34)			348	(11)			419	(2)
13	393	(7)	420	(3)	358	(20)	361	(40)			358	(11)				
14					364	(12)	383	(40)			342	(6)				
15					388	(4)	398	(20)			373	(3)				
16							398	(11)			353	(2)				
17							410	(7)			366	(4)				
Total (N)		137		96		180		269		69		136		56		59

ray, longest pelvic spine, and the longest pelvic ray following the procedure described by Phillips (1957); the longest dorsal ray, longest dorsal spine, the lengths of the three anal spines, and the longest anal ray measured from the posterior point of insertion, the longest gill raker on the first arch, body depths at the ventral fin and anal fin, and distance between the anal pore and the anterior insertion of the anal fin following the method of Holt (1959).

Morphometric measurements were subsampled for fish from throughout the size ranges used in the age-length determinations. An attempt was made to measure five fish from each centimeter-interval of total length so that 100–200 fish of each species were represented in the sample. Regressions were used to determine the relationships between 23 body parts regressed against standard length. Analysis of covariance was used to test for significant differences ($P<0.01$)) in the body parts between males and females.

Ontogenetic changes in proportions of the 23 body parts regressed against standard length were also evaluated. By taking the mean standard length at each age from the age-length curve and the regressions the body part size at each age was estimated.

A computer program for discriminant analysis (Nie et al. 1975) was used to determine the probability that sex could be identified, for a particular species, when given only body-part measurements.

Results

In all four species, females were larger than males of the same age after 5–7 years of age (Table 1). The differences were only significant ($P<0.01$) in the blue rockfish, however, a trend can be seen of females getting bigger and living longer than the males even with the small sample size used. This trend agrees with other growth studies for these species (Miller & Geibel 1973, Six & Horton 1977, Love & Westphal 1981).

The linear regressions for the morphometrics showed that a number of body parts differed significantly between the sexes ($P<0.01$) (Table 2). When 23 independent measurements are analyzed for significant differences there is a fairly high probability that, by chance alone, at least one measurement will show significant differences:

$$P = 1-0.99^{23} = 0.21.$$

The probability of two or more significant differences due to chance alone is considerably lower:

$$P = 1-0.99^{23} - \frac{23!}{22!} (0.01)(0.99)^{22} = 0.02.$$

This study showed two to four significantly different body parts per species (Table 2). Body parts which differed by sex in at least one species were: upper jaw length, pelvic spine length, longest anal ray, first anal spine length, longest dorsal ray and orbit width. Two of these body parts were significantly different in at least three of the species (Table 2). The orbit width which was larger relative to standard length in males of all four species, and the longest pectoral fin ray was larger relative to standard length in males of the black, yellowtail and olive rockfishes. Sexual dimorphisms do exist in additional species of *Sebastes* than previously documented (Chen 1971) although the differences are slight (Echeverria 1980).

Ontogenetic studies showed a proportional increase in length or width with respect to growth and these changes often differed for the two sexes. For example, a longer upper jaw and a longer anal spine occurred in males of *Sebastes melanops*. The striking finding was that, in all four species studied, the orbit width and the pectoral fin ray length were related to age so that males and females of the same age had orbits the same width and pectoral fins rays the same length (Table 2). These results indicate that there are some real, although subtle, differences in the growth rates of some body parts.

Discriminant analysis yielded correct assignments of fish to sex of 70% of black rockfish, 75% of yellowtail rockfish, 89% of blue rockfish and 79% of olive rockfish (Table 3). All fish in the analysis were used to estimate the discriminant function; then each fish is assigned a sex based upon the measurements of certain body parts and their respective discriminant values. A sample of fish not used in the analysis were assigned sex based on the relevant body parts. Correct assignments of fish to sex were 74% in black rockfish, 80% in yellowtail rockfish, 92% in blue rockfish

Table 2. Significant ($P<0.01$) sexual dimorphisms in the size of body parts, as related to standard length and to age, in four species of *Sebastes*. In the case of significant differences, the sex with the larger body part is listed.

Body part	*S. melanops*	*S. flavidus*	*S. mystinus*	*S. serranoides*
Anal spine 1				
age				
SL	male			
Pelvic spine				
age		male		
SL		male		
Pectoral fin ray				
age		male		
SL	male	male		male
Anal depth				
age			female	
SL			female	
Anal ray				
age			female	
SL			female	
Dorsal ray				
age			female	
SL			female	
Orbit width				
age				
SL	male	male	male	male
Upper jaw				
age	female			
SL	male			

and 60% in olive rockfish (Table 3). It is clear that there are some statistically significant differences in the body proportions, but, because of the variability in the measurements, and the values of percent agreement, no combination of the measured body parts can be used to adequately predict the sex of these fish.

Rockfishes tend to aggregate by species with the sexes in the same aggregations. Hallacher (1977) studied kelp-bed inhabiting species of rockfishes and found that each species apparently occupied a particular space in the water column with regard to depth and bottom type. In addition to having various spacial localities the species occur in different geographic areas. On the sport-fishing trips sampled in this study, the species were not of equal abundance at the various collection localities (Table 4). When a species occurred both sexes were present. The sampling technique does not allow for a critical examination of the relationship between the sexes in an aggregation. There is no indication that males and females segregate into different areas, however, the sex ratios may exhibit some seasonal variability. It appears that, for the most part, both sexes of a species inhabit the same area, occurring together in aggregations.

Discussion

The study of a species' morphology can provide insight into its natural history, particularly with regard to selective pressures in its environment. In this study, 23 key morphological features of four species of rockfish were examined in an attempt to identify previously undescribed sexual dimorphisms. These morphological data, when combined with known aspects of the life history of these species, provide clues to the evolution of sexual dimorphism in rockfishes.

Sexual size dimorphism is usually attributed to sexual selection, having evolved with respect to

Table 3. Discriminant values used to assign sex from morphometric data in four species of rockfish, the percent predictability from the analysis, and a test sample of other fish.

Body part	Discriminant value
S. melanops	
predictability (N = 136) = 70%	
test cases (N = 31) = 74%	
Standard length	0.0424
Orbit width	0.1303
Upper jaw	0.1117
Pectoral ray	−0.2024
First anal spine	−0.2658
constant	4.1921
male centroid	−0.5215
female centroid	0.3622
S. flavidus	
predictability (N = 113) = 75%	
test cases (N = 24) = 80%	
Standard length	−0.0609
Pectoral fin	−0.1524
Orbit	−0.1674
Pelvic spine	0.1590
constant	3.4183
male centroid	−0.5471
female centroid	0.4471
S. mystinus	
predictability (N = 193) = 89%	
test cases (N = 45) = 92%	
Anal depth	−0.1416
Orbit	0.3884
Dorsal ray	0.0935
Standard length	0.0019
Anal ray	0.0096
constant	6.9223
male centroid	1.5198
female centroid	−1.0573
S. serranoides	
predictability (N = 127) = 79%	
test cases (N = 20) = 60%	
Standard length	0.0601
Pectoral ray	0.1437
Orbit	−0.1377
constant	−4.5387
male centroid	−0.5634
female centroid	0.8628

Table 4. Distribution of the sample for the four species of rockfish used in the age-length study; the area they were fished and the number of males (M) or females (F) sampled.

	Point Reyes		Farallon Is.		Cordell Bank	
	M	F	M	F	M	F
S. melanops	137	96	0	0	0	0
S. flavidus	24	49	46	98	119	113
S. mystinus	38	64	31	72	0	0
S. serranoides	2	4	51	53	3	2

reproductive success. This is observed in many mammals where larger males have evolved due to competition for females (Darwin 1871). In the rockfishes studied here, males were smaller than females, which is often the case with invertebrates (Darwin 1871) and many poikilotherms (Shine 1979, Ghiselin 1974), where sexual selection favors males diverting energy from growth into reproduction at an earlier age than females.

Sexual size dimorphism has been shown to occur in many species where there is a different age of maturity for males and females (Wilson 1975). In some species, size dimorphism has been correlated with a later onset of maturity in males (Wiley 1974, Ghiselin 1974). In rockfishes exhibiting size dimorphism the situation appears to be reversed. Where size dimorphism occurs in *Sebastes* males are smaller than females, with different growth rates between males and females tending to occur after the fish are 6 to 8 years old (Westrheim & Harling 1975). For the yellowtail rockfish, *S. flavidus*, sufficient data exist to correlate the differential growth rates with sexual maturity. Using information from the same sample of yellowtail rockfish, Fraidenburg (1980) obtained growth curves and Gunderson et al. (1980) obtained size at sexual maturity. On the average, male yellowtails mature at 407 mm fork length and 8 years of age. Females mature later, when they average 450 mm fork length and 10 years of age. The size of an average 10 year old male is about 430 mm. Growth slows down at maturity so that males grow more slowly after 8 years whereas growth in females does not slow until around 10 years. After the initial change in growth rates an average difference of about 20 mm remains constant, which agrees with results found for yellowtail rockfish examined in this study (Table 1). Growth curves for the other species in this study show that males are smaller than females. This occurs after age 7 in black rockfish (Six & Horton 1977), after age 5 in blue rockfish (Miller & Geibel 1973), and after age 4 in olive rockfish (Love & Westphal 1981). Sexual size dimorphism in black, blue and olive rockfishes probably also correlates to differing ages at which sexual maturity is attained by males and females.

The widespread occurrence of sexual selection and its effect on sexual dimorphism is often related to a species' mating system and the degree of parental investment (Wilson 1975). The evolution of parental care results in an increase in the survival of young (Balon 1984). Perrone & Zaret (1979) proposed that parental care by males occurs when paternity is insured, as in nestspawning fishes where the male guards the nest of eggs after fertilization. Parental care by females usually occurs before fertilization while yolk reserves are built up, or after fertilization if she retains the fertilized eggs.

Larger females and smaller males in *Sebastes* can be understood in terms of differential parental investment. Females, by retaining the fertilized eggs until young are ready to actively feed orally, contribute to the care and protection of the young. Also, the numbers of eggs produced increases with size; therefore, larger females release more young and contribute more to the gene pool. Natural selection favors larger females. In *Sebastes* with internal fertilization and retention of the embryos, the female makes the greatest parental investment, with investment by males limited to contributing sperm.

Sexual size dimorphisms are predicted by Trivers' (1972) theory which suggests, for homeotherms, that males will compete among each other for females if females are more involved with the offspring's survival than males. This results in males being subject to selective pressures directly related to this competition, with larger more aggressive males being favored. Observations of premating by the blue rockfish did not indicate aggressive behavior among males (Helvey 1982), suggesting that sexual size dimorphism in *Sebastes* does not result from male competition for females. There is, however, another possible battleground besides aggressive behavior among males, and that is if the opportunity exists for the sperm to compete. In *S. alutus* there is a possibility that multiple mating occur (Lisovenko 1970). Males may thus be competing by copulating more frequently. With multiple mating and the storage of sperm by females, intraovarian competition between the sperm of different males may contribute to the earlier maturity of males, the advantage of being reproductive earlier relating to sperm production and outweighing any disadvantage related to smaller size (Warner & Harlan 1982). Warner & Harlan suggest sexual selection is responsible for the smaller size of males in the livebearing dwarf surfperch, *Micrometrus minimus*. Similar sexual selection may be responsible for the smaller males found in some species of *Sebastes*.

Sexual dimorphisms exhibited as morphological differences have recently been shown to exist in groups of marine fishes previously not known for dimorphic features (Gordina et al. 1974, Grant et al. 1977). The differences in body form in the species studied here were slight, but statistically significant, and were a result of different growth rates of the body parts.

The disproportionate body parts in male *Sebastes* cannot, based on the available evidence, be firmly attributed to sexual selection. The relatively large eye might be useful in locating females or perceiving visual displays for mating. Fin dimorphisms may be used in sexual displays; however, not enough is known about the behavior of *Sebastes* spp. to relate these differences to sexual behavior. Perhaps they evolved not from sexual interactions but from sexes of different sizes occupying the same habitat, that is, males coexisting with females larger than themselves. How the dimorphisms relate to possible functional advantages will be discussed for the two most common dimorphisms, the orbit width and the length of the pectoral fin ray.

Growth rate of the orbit is equal in males and females (Table 2). Since females grow faster, males have a larger orbit for their size. If the width of the orbit reflects the overall size of the eye, then the eye in males and females of the same age is comparable regardless of the size of the fish. The internal structure of the eye varies widely among species of fishes and is adapted to a particular habitat (Munz 1971). The organization of a fish's eye varies to perceive size, brightness, color, distance, orientation, and motion (Ingle 1971). Predaceous fishes, for instance, have larger eyes which increases visual acuity enabling them to detect motion better (Walls 1967). In the black, yellotwail, blue, and olive rockfishes the eyes of males, although proportionately larger, are probably functionally equivalent to females of the same age. This suggests strong selective pressure favoring visual 'equivalence' between the sexes, presumably related to foraging and avoiding predators.

In higher teleosts, the main functions of pectoral fins are to control orientation during swimming, to maintain a stationary position in the water column (less important in fishes with swim bladders such as *Sebastes*), and to accelerate from a standing start (Gosline 1971). Species of *Sebastes* that aggregate in the water column frequently hover in one location (Hobson & Chess 1976, Hallacher 1977, Moulton 1977). In this situation, the pectoral fin may be used to remain stationary within an aggregation and to assist in thrusts toward prey. Presumably thrust speed would be less important to planktivores (blue rockfish) and, accordingly, may account for pectoral fin ray dimorphism occurring only in the three more piscivorous species (black, yellowtail, and olive rockfishes). The pattern suggests that this characteristic may be a response to the smaller males' need to compete with larger females for elusive prey since they apparently aggregate together (Table 4). In fact, the black rockfish (Moulton 1977), the yellowtail rockfish (Pereyra et al. 1969), the blue rockfish (Miller & Geibel 1973) and juvenile olive rockfish (Hobson & Chess 1976) primarily aggregate by species.

Separation of the sexes for part of the year occur in *S. marinus* (Sorokin 1961) and *S. alutus* (Westrheim 1970, Gunderson 1974). Possible spawning migrations for the black rockfish was indicated by four females in the gravid and recently spawned condition collected offshore in the central north Pacific (Dunn& Hitz 1969). Since the evidence is sparse that the sexes do separate, the species in this study probably co-occur, feeding, seeking shelter, and avoiding predators together.

Since all four species form aggregations; the advantages of associating appear to outweigh disadvantages that may arise due to size disparity between the sexes in the same aggregation. Aggregations are a good defense against predators, providing a confusion of darting bodies that makes it difficult for a predator to home in on a particular prey (Hobson 1978). Being in aggregations also increases the habitat available to a species; hiding places are not necessary because the aggregation serves the purpose (Hamilton 1971). Finally aggregating also helps keep the sexes together during a long mating season. Courtship and insemination in *Sebastes* apparently occurs over a period of at least a month, with extrusion of the young in any one species occurring during at least a 2 month period.

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86144

Marine Debris: A Growing Concern

By Howard O. Yoshida

Entanglement and suffocation by plastics, capture by "ghost fishing" gill nets, or death from discarded glass, metal, wood and rubber trash are constant threats to marine life. Scientists, conservationists and environmentalists are worried about the future of the sea.

A Workshop on the Fate and Impact of Marine Debris was held in November 1984 at the Ala Moana Hotel in Honolulu, Hawaii. Approximately 125 individuals including scientists and interested persons from Japan, Republic of China (Taiwan), United Kingdom, Republic of Korea, Canada, New Zealand, Federal Republic of Germany, and the United States participated in the workshop. Also, about 16 environmental-conservation type organizations were represented.

An uninformed layman could ask, what's so interesting about marine debris, and who cares what happens to it? For the past 10 years or so, marine scientists, conservationists, environmentalists, and others have been worried about the greatly increased amounts of marine debris that are apparent in the oceans around the world. The marine debris of much concern consists of lost and discarded fishing gear and other materials unrelated to fishing such as cargo nets and packing bands. The debris, a form of marine pollution, may be an especially serious problem in the North Pacific Ocean where it contributes to the deaths of marine animals: marine mammals, particularly the northern fur seal, *Callorhinus ursinus*, and the Hawaiian monk seal, *Monachus schauinslandi*, marine turtles, seabirds, and fishes. Marine debris also poses a threat to human safety by fouling the propellers of vessels.

The objectives of the workshop were to (1) review the state of knowledge on the fate and impact of marine debris to determine the extent of the problem; (2) identify and make recommendations on possible mitigating actions; and (3) identify and make recommendations on future research needs. The workshop opened with a review of conventions, laws, and regulations that could provide a legal framework for resolving the marine debris problem. This was followed by technical sessions on the source and quantification of marine debris: the impact of debris on marine resources; and the fate of marine debris in the oceans; and a general session to focus on identification of management needs.

The complete results of the workshop are contained in the "*Proceedings of the Workshop on the Fate and Impact of Marine Debris, 27-29 November 1984, Honolulu, Hawaii,*" a 580-page document that was published under the auspices of the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA. The document includes all the scientific and technical papers that were presented at the workshop plus summaries of the discussion sessions, and is probably the most comprehensive compilation of information, under one cover, on the subject of marine debris and some of its impacts to date. This article briefly treats the contents of the Proceedings of the workshop. A person interested in more detailed information on the marine debris problem should refer to the Proceedings.

Background: Debris Reported in '30's

The entanglement of marine animals in debris apparently is not a new phenomenon. There are reports of the entanglement of northern fur seals in debris on the Pribilof Islands in the 1930's. In these early incidents the seals were entangled in rubber bands cut from the inner tubes of automobile tires. In the 1960's it was noticed that increased numbers of northern fur seals were being entangled – this time in material lost or discarded by fishing vessels and merchant ships. It also became apparent that the problem of entanglement was not confined to northern fur seals but it also affected other marine mammals, including the Hawaiian monk seal (a species listed as an endangered species under the Endangered Species Act), sea lions, harbor seals, and northern elephant seals. Marine debris also entangled seabirds, sea turtles, and fishes. Furthermore, the problem had other facets: seabirds and sea turtles, for example, feed on debris such as plastic bags, small plastic pellets, and other man-made material. Although most of the observations on marine debris related problems have been made in the North Pacific, observations from other areas indicate that the problem is worldwide.

Marine debris is composed of a wide variety of objects including glass, metal, wood, rubber, and plastics. Plastics are probably the most persistent component of marine debris and material that causes the most

Photo by Susan R. Lautenslager

In the northwestern Hawaiian Islands the surrounding ocean currents may bring lost or discarded gill nets from mid-ocean squid fisheries and trawl net fragments from the North Pacific groundfish fisheries. John R. Henderson, a fishery biologist with the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, hauls in fragments of fishing gear near one of the islands.

problems. Although the sources of debris in general, and plastics in particular, are many and varied, a large amount of persistent plastics appears to originate from the fishing industry.

Quantification of Marine Debris

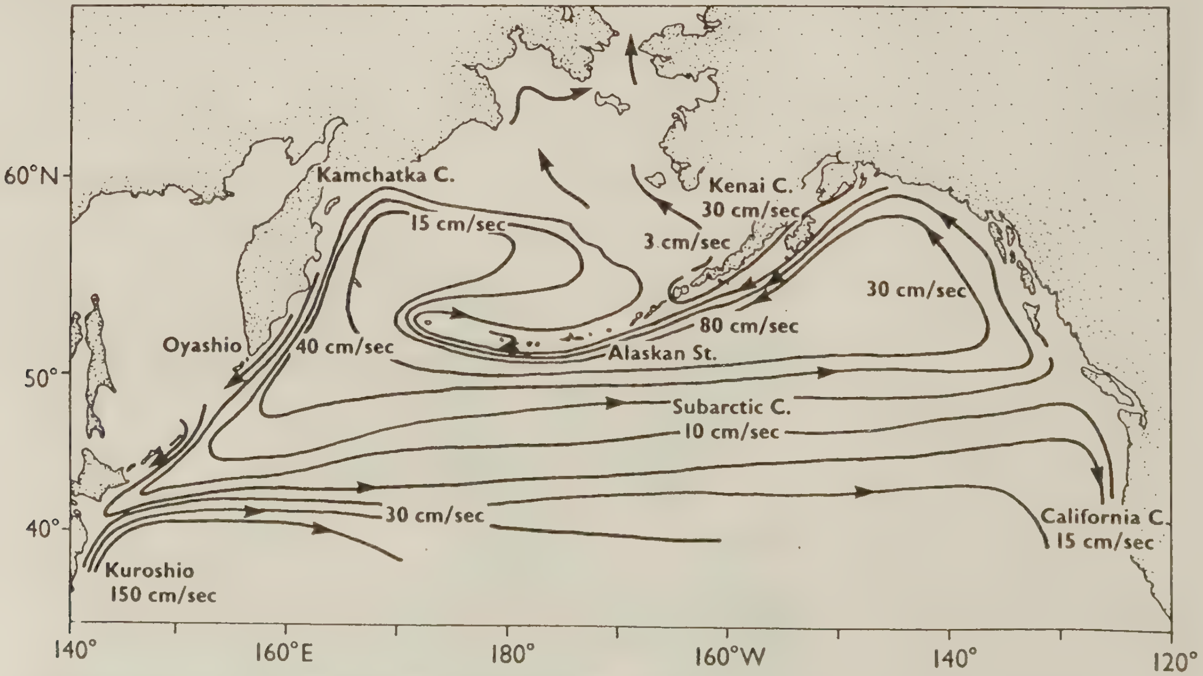
To provide background information for the discussions on marine debris, reports describing the fisheries and fishing effort were reviewed. An idea of how plastics (e.g., polyethylene and other fishing nets and lines) become part of the marine debris can be obtained by the extent of fisheries in the oceans. The Taiwan high seas gill net fishery for squid in the North Pacific is located between lat. 35° and 45°N and long. 152° and 158°W. The Korean gill net fishery for squid in 1981 stretched from lat. 34° to 46°N and long. 142°E to long. 179°W; in 1983 this fishery expanded to the east of long. 165°W. It is estimated that the Korean gillnetters used 139,638 to 4,070,372 units of gill nets (one unit is 50 by 8 meters or 164 by 26 feet) annually from 1980 to 1983. The Japanese have trawl fisheries in the Bering Sea, Gulf of Alaska, northwest Pacific, and the North Pacific. They also have mothership and land-based salmon drift gill net fisheries in the Pacific, a squid drift gill net fishery, and a gill net fishery for marlin and other species. It is estimated that, on the average, trawls of various sizes are fished 71,900 to 94,000 times per year in the Japanese trawl fisheries in the Gulf of Alaska and Bering Sea. In the various Japanese drift gill net fisheries in the North Pacific, the total combined length of all the gill nets fished during a year is estimated to be 1,409,270 km (875,704 miles), on the average. It has been estimated strung end to end there are 170,000 km (105,638 miles) of gill nets available in the North Pacific fisheries at any one time. This amount of net can circle the Earth at the Equator approximately 4.2 times.

Another way to examine the potential problem on loss of fishing gear is to determine the amount of fishing effort in the various fisheries. For example, fishing (mostly exploratory and limited scale) by non-U.S. (predominantly Japanese) trawlers in the Bering Sea-Aleutian Islands area began in 1954. From the late 1950's to the early 1970's there was a severalfold increase in fishing effort. In the past 10-12 years, the effort has remained near the highs of the early 1970's, and in recent years the U.S. vessels in the domestic and joint venture fisheries accounted for an increasing fraction of the total effort.

In the northeast Pacific, a non-U.S. trawl fishery for groundfish started in 1962. The fishing effort fluctuated up and down and reached a record peak in 1975, but has since fallen sharply. Joint venture fishing by U.S. vessels, and to some extent similar ventures by Canadian vessels, have offset a substantial amount of reduced non-U.S. fishing effort. Currently, the combined effort by non-U.S. joint fisheries is about 55% of the 1974-76 peak of the non-U.S. trawling effort. It is estimated that the total annual trawl effort for non-U.S., U.S., and joint venture fisheries in the Bering Sea-Aleutian Islands area, and U.S. and Canadian trawl groundfish fisheries in the British Columbia-California area was 234,000 to 794,000 hours, on the average, between 1956 and 1983. It would take about 27 to 91 vessels fishing every day of the year, 24 hours per day, to accumulate 234,000 to 794,000 hours of fishing.

Attempts were also made to estimate net loss in the trawl fishery for groundfish off Alaska. From 1960 to 1969, 14-27 nets or pieces of nets were lost in the Bering Sea-Aleutians-Gulf of Alaska trawl fisheries. From 1970 to 1979 the loss was 20-27 nets or pieces of nets, and from 1980 to 1983 it was 35-65. The difficulty in determining the reality of the estimates of net loss was pointed out because among other things, the numbers were extrapolated from direct observations made in 1983 only.

Another way to shed some light on the problem was to estimate the density of discarded and lost fishing gear in the ocean. First approximations were made on the density of the type of debris that was affecting the northern fur seal in the eastern North Pacific and Bering Sea. In the eastern North Pacific and Bering Sea it is estimated that there is one fatal encounter of a northern fur



A large amount of the debris in the oceans originates from fishing and maritime vessels. It has been estimated that over seven million tons of waste materials are discarded in the oceans each year from ships. A knowledge of the surface ocean currents provides good guesses as to where buoyant trash dumped in the ocean will eventually end up. The chart of the currents in the subarctic Pacific Ocean shown here is from the paper, "On the general circulation in the subarctic Pacific," by Donald K. Reed and James D. Schumacher.

seal pup per 18,600-93,000 nautical miles of travel, or one fatal encounter with webbing per 200 to 100,548 square nautical mile of water searched by the seal pup (average of 4,484 square nautical miles). It was also estimated that there would be one unit of webbing of the dangerous mesh size (20-25 cm or 8-10 inch stretched mesh) per 3,342-6,683 square nautical mile (average of 4,726 square nautical mile). According to the author of the report, that density of webbing appears to be low, but there appears to be enough discarded and lost webbing to cause the estimated mortalities of northern fur seals. Much of the deaths takes place in the first two years of a seal's life, and it has been estimated that the population of northern fur seals has been declining at approximately 4-8% per year for the past 10 years.

Direct observations have been made on the amount, types, and distribution of debris in the ocean. During one period of observation in the western North Pacific from 1978 to 1983, a trawl net fragment and a gill net fragment were seen in about 196 hours of direct observations over a distance of about 1,768 nautical miles. In 1984, during about 973 hours of direct observations covering 7,559 nautical miles in the western North Pacific and 1,200 nautical miles in the Bering Sea, three 2-meter (6.5 feet) trawl net pieces were seen. Also nine pieces of gill net fragments of about half a meter to 150-meter (2-492 feet) long were seen. In addition, net debris comprising fragments of 4 trawl nets and 20 gill nets was seen in incidental observations. Three northern fur seals were entangled in two of the trawl net fragments. Two northern fur seals, one salmon shark, *Lamna ditropis*, 11 birds of various species, and an undetermined number of salmon were entangled in the gill net fragments. The amount of net debris and the associated entanglements were considered to be low and could have been due to the difficulty in sighting or of the infrequent presence of debris. In similar type of observations, estimates of the average density of marine debris larger than approximately 2.5 cm^3 (0.15 $inch^3$) of 0.28 per km^2 (0.4 square mile) were obtained between lat. 38° and 56°N and 3.73 per km^2 (0.4 square mile) in lat. 21°-39° and 27°-42°N.

It is estimated that 6.4 million metric tons (7.1 million tons) of material is discarded annually from ships, and in waters around Alaska, about 1,664 metric tons (1,834 tons) of plastic litter is lost or discarded annually from fishing vessels. An unknown fraction of marine debris in the ocean finds its way to shore. To determine if beach surveys are good indicators of oceanic litter the quantities of fish net fragments and other plastic litter were determined on Alaska beaches by foot surveys from 1972 to 1984. Some of the conclusions reached in this study were that most of the litter were from non-U.S. fisheries, and fragments of trawl netting always constituted the bulk of the debris by weight. Also, a decrease in debris on Amchitka Island between 1974 and 1982 was attributed to the smaller number of vessels fishing off Alaska, which indicated that marine debris could be rapidly reduced if disposal could be controlled at sea.

Impacts of Marine Debris on Wildlife

Although the quantitative aspects of the interaction of wildlife with marine debris are not well understood, it is apparent that a wide variety of marine wildlife interacts with debris. Interactions of marine debris with marine mammals, birds, fishes, and turtles were described in reports presented at the workshop.

Intensive observations on entanglement of northern fur seals were started on St. Paul Island, Alaska in 1981, including those on the kinds of entangling debris, the manner of entanglement, the condition of the affected seals, and the frequency of entanglenent by age and sex of seals. Most of the seals that were found to be entangled were entangled in large mesh trawl net fragments. The next most frequently seen entangling debris were plastic packing bands. Other entangling debris noticed included ropes, strings, rubber bands, plastic rings, and metal headlight rings.

These studies indicated that fur seal mortality rates resulting from entanglement may not be as high as had been assumed. For example, the assumption that seriously injured seals would die in a short time were not supported by observations made during this study. Nevertheless, other studies showed that the mortality rates caused by entanglement were consistent with those which would cause the present population trend. It was pointed out, however, that although entanglement appeared to be an important factor, accurate estimates of deaths caused by entanglement were not available.

Observations on Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska and southeastern Alaska showed that these animals also become entangled primarily in packing bands and net fragments. Also, although encounters with marine debris could be confirmed as the cause of entanglement in only a few instances, trawl net fragments and plastic packing bands were confirmed as the entangling debris in a study on northern elephant seal, *Mirounga angustirostris*, California sea lion, *Zalophus californianus*, and harbor seal, *Phoca vitulina richardsi*, at San Nicholas and San Miguel Islands, California.

Off the coast of Oregon the number of marine mammals interacting with marine debris appeared low during observations made since 1968, although entanglements in actively fishing gear have been reported. The animal most frequently involved in encounters with fishing gear was the gray whale. In these encounters the most frequent observation was the snagging of commercial crab pot buoy lines in the jaws of the whales.

In the Northwestern Hawaiian Islands 27 indidents of entanglements by Hawaiian monk seals have been documented through 1984. Also, at least eight additional seals had scars resulting from entanglement. It was speculated that the entanglement was fatal to at least one seal, and that six seals would have probably died if biologists had not intervened. Most of the entanglements of Hawaiian monk seals involved pups. Although weaned pups constitute only about 11% of the population of seals in the Northwestern Hawaiian Islands, they were involved in 41% of the entanglement incidents.

Although the workshop dealt primarily with marine debris in the North Pacific, reports of the interaction of wildlife and marine debris from elsewhere in the world were presented. In New Zealand waters a marked increase in such encounters were observed since 1975. The New Zealand fur seal, *Arctocephalus forsteri*, is now frequently seen with polypropylene strapping bands, usually around the neck. Fur seals have also been seen entangled in discarded fishing nets. Hooker's sea lion, *Phocarctos hookeri*, has also been seen with netting around the neck. A killer whale, *Orcinus orca*, and a southern right whale, *Eubalaena australis*, died as a result of entanglement in fishing gear. A juvenile minke whale, *Balaenoptera acutorostrata*, which became stranded and died had a compacted plastic bag stuck in the esophagus, which was probably the cause of its death. A leatherback turtle, *Dermochelys coriacea*, which beached itself and died had plastic bread bags packed in its esophagus.

To date 50 species of seabirds are known to feed on plastics. The albatrosses, fulmars, and petrels feed on plastics most frequently, and phalaropes (small pelagic shorebirds) and some auk, murre, puffin, etc., type seabirds also have relatively high rates of feeding on plastics. The two major types of plastics ingested by seabirds are plastic fragments and raw plastic pellets, and it appears that the principal sources of plastic fragments are the solid wastes and plastic objects discarded from fishing boats and merchant ships at sea. Also, some of the

Photo by John R. Henderson

In addition to fish and marine mammals, sea turtles also become entangled in marine debris. This green turtle was found entangled in rope and net debris in the northwestern Hawaiian Islands.

plastics found nearshore come from nearby population centers. The effects of the ingestion of plastics by seabirds are not fully understood. It is believed that for most species of birds the rates of feeding and the amounts of plastic fed on are low enough that there is no deleterious effect on the birds. Several species of seabirds, however, show high enough rates of feeding on plastics to cause concern. It has been suggested that high ingestion of plastics may have a detrimental effect on breeding.

Published records indicate that five sea turtle species have fed on various types of marine debris. The green turtle, *Chelonia mydas*, constituted 32% of these records, followed by the loggerhead turtle, *Caretta caretta*, (26%), leatherback turtle (24%), hawksbill turtle, *Eretmochelys imbricata*, (14%), and Kemp's ridley turtle, *Lepidochelys kempi*, (4%). Immature turtles more frequently fed on debris than the adults in four of the five species. The turtles most commonly fed on plastic bags and sheets (32%), followed by tar balls (21%), and plastic particles (19%). Other items ingested by the turtles included cloth, fishing net, paper, glass, and metal. Also, the green, loggerhead, hawksbill, olive ridley, and leatherback turtles have been entangled in debris. The green turtle accounted for 42% of the records. Debris responsible for the entanglements was monofilament fishing lines (33%), rope (23%), pieces of trawl net (20%), and nonfilament net (13%).

In addition to all the entanglement of wildlife discussed above, fishing gears such as gill nets continue to catch the species of fish (and other fishes) they were set for even after they become derelict (ghost fishing). Experiments with commercial style crab pots showed that up to 55% of sublegal Dungeness crab, *Cancer magister*, remained in the traps after 12 days, and 17% of these crabs died. Observations on several pieces of derelict salmon gill nets showed that fish and diving birds continued to be caught for more than 3 years, and crabs continued to become entangled after 6 years. Other ghost gill nets contained live or decaying Atlantic cod, *Gadus morhua*, Atlantic wolffish, *Anarhichas lupus*, spiny dogfish, *Squalus acanthias*, winter flounder, *Pseudopleuronectes americanus*, American lobster, *Homarus americanus*, and crabs.

Fate of Marine Debris

As indicated earlier, one of the goals of the workshop was to determine the fate of marine debris, that is, what happens to the long lasting plastics and other material once they are discarded or (for fishing gear) are lost and become derelict. It is obvious that surface ocean currents would have the greatest influence on floating objects in the sea, and so would provide the best clues as to the fate of marine debris. With this in mind the workshop participants reviewed the surface currents and current systems in the North Pacific and adjacent areas. Also discussed was the "population dynamics" of marine debris, such as how much debris are entering the "population" and how much are leaving per unit time.

The study of ocean currents has progressed from direct ship-drift observations to indirect theoretical computations, and to direct current measurements by current meters and satellite tracking of drifting buoys with attached drogues. Charts of the ocean currents based on ship-drift determinations produced in 1935 show the general circulation as it is known today. In the Pacific Ocean the major currents are the northeastward flowing Kuroshio and the eastward flowing North Pacific Current in the western Pacific. In the eastern side of the Pacific, the North Pacific Current splits into the Alaska current which flows north and the California Current which flows south. The westward flowing South Equatorial Current is between about lat. 5° and 10°N. More recently oceanographers have progressed from describing steady state and average ocean currents to describing the variability of currents. One report presented at the workshop described the general surface water circulation and seasonal variations in the circulation in the subarctic Pacific (lat. 40°N to the Bering Strait). It pointed out that the Subarctic Current is a slow eastward drift but that in the winter its speed increases fourfold as a result of strong winds blowing eastward. Other seasonal variations in current systems within this region were also examined. It also provided a chart showing the "climatological mean surface circulation" in the subarctic Pacific including the speeds of the various currents.

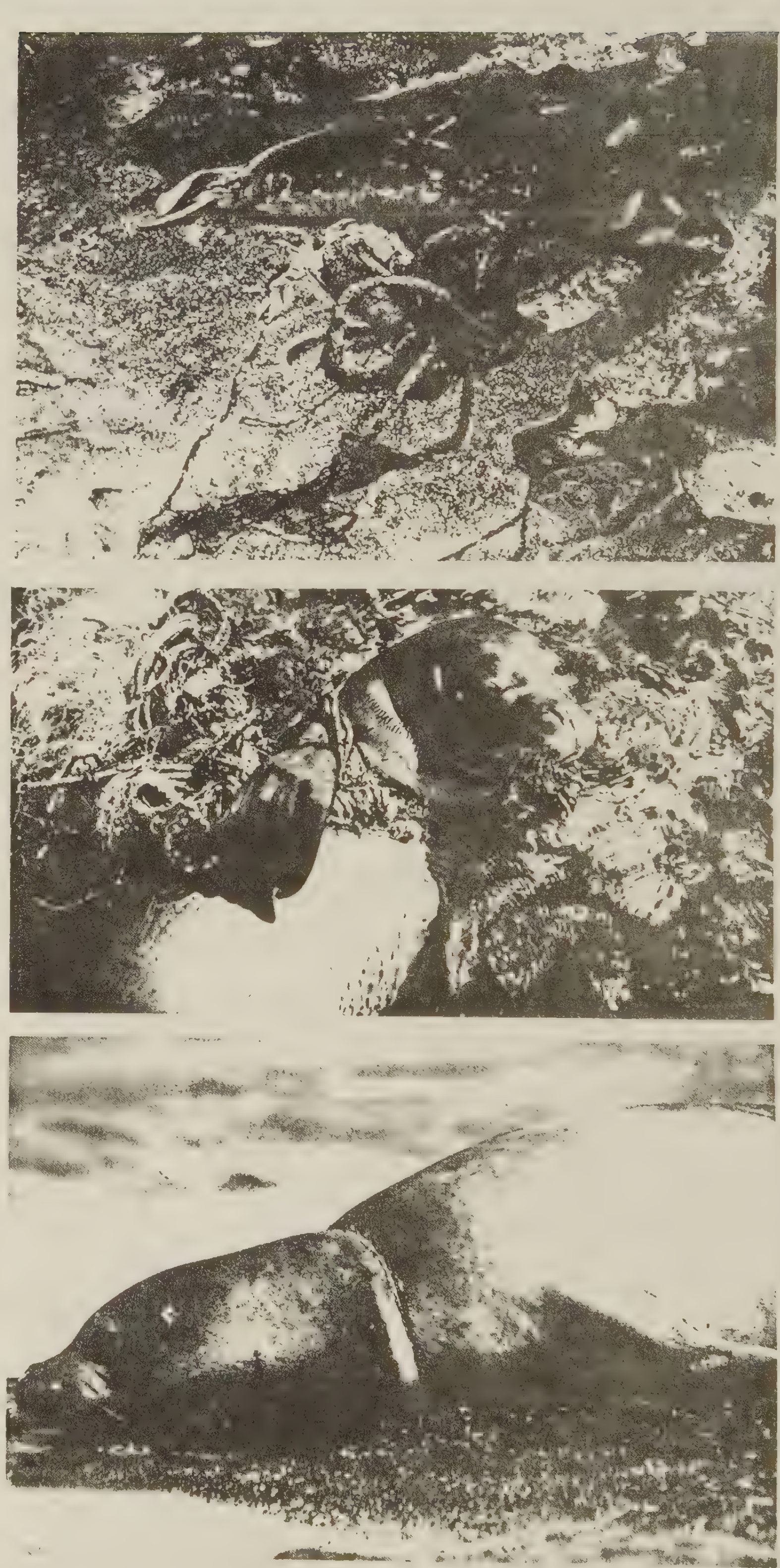
All the charts described above, however, only provide gross or average pictures of the ocean circulation in the Pacific Ocean. They do not provide information on eddies or periodic fluctuations and interannual variations of the currents. To predict the likely movement of marine debris on the ocean surface, it would be desirable to have current forecasts similar to weather forecasts. Without such current forecasts, however, the estimates of the mean climatological surface circulation may be useful in making general predictions on the fate of marine debris. Based on these charts, for example, it can be predicted that debris entering the ocean off northern Japan should arrive off the west coast of the U.S. in about 2 years.

Solution to the Problem

Although marine debris is undoubtedly a problem throughout the world's oceans, the workshop concluded in part that more data and information were needed on the quantity, type, distribution, and change with time of the amount of debris in the oceans. The consequence and quantitative impacts of the interaction of marine animals with debris did not appear to be well understood and documented, although qualitative information showed that deaths of marine animals attributable to marine debris in addition to those caused by natural factors are evident. It was further recommended that studies be initiated to estimate the timing and rates of change of the threat of marine debris, that is, how does debris change mechanically, for example, how nets become balled up; chemically (chemical effects on buoyancy), and biologically (the effects of plant and animal growth on debris). Educational programs should be started to change human attitudes toward the environment, that is, the oceans (even at their greatest depths) and beaches are not limitless garbage dumps, and to encourage and facilitate the proper disposal of debris. Educational programs directed particularly at the world's fishing and maritime community, national and international organizations, and plastics industries are needed to communicate the extent of the marine debris problem. Research should be conducted to determine if materials that may potentially become marine debris can be made degradable.

With regard to some of the marine animals that are affected by marine debris, the primary problem for the fur seals appeared to be trawl net fragments and plastic bands. Research is needed to confirm mortality rates caused by such debris that to date have been estimated by indirect methods. For the monk seals in the Northwestern Hawaiian Islands, trawl net fragments were perceived to be the main source of possible deaths. The mortality rate for monk seals attributable to marine debris is unknown but any loss to this endangered species is serious. Research needs for the monk seal are much the same as for fur seals. As for seabirds, marine debris affects seabirds in two ways: through ingestion of plastics and entanglement. Because the effects of the ingestion of plastics by seabirds are not well understood, physiological studies and experiments are needed to determine such effects. Although sea turtles have been entangled in marine debris, the more serious potential problem appears to be the ingestion of plastics and other debris. Similar studies on the physiological effects of plastics on sea turtles are needed.

HOWARD O. YOSHIDA
is a fishery biologist with the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Department of Commerce. He has a B.A. degree in zoology from the University of Hawaii. He has authored and coauthored more than 30 scientific and technical papers on fishery biology and fishes in the Pacific Ocean, and has participated in numerous fishery expeditions in the central and South Pacific Ocean. He presently holds the position of Chief, Publication Services at the Honolulu Laboratory.



Photos by John R. Henderson, Doris J. Alcorn and William G. Gilmartin

Pups of the Hawaiian monk seal are susceptible to entanglement in fragments of fishing gear and other debris that wash ashore. During 1984, 27 incidents of monk seal entanglement in debris were documented in the Hawaiian Islands. The lower picture shows an injured monk seal with a scar around the neck from an unidentified constricting material. Plastic packing bands are frequent causes of such scars on seals.

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Year-Class Strength and Survival of O-Group Clupeoids[1]

Paul E. Smith

Southwest Fisheries Center, La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, USA

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Global marine fish catch has been stable over the past decade but the clupeoid contribution has declined from one-half to one-third of the marine fish catch. This decline appears to be caused by changes in recruitment success during heavy fishing pressure. Theoretical population approaches and correlative environmental indices are not yet sufficient for setting catch limits. For some time the direct measurement of current biomass appears to be necessary for setting clupeoid quotas. Precision and cost studies on the estimation of biomass with current methods indicate that a standard error of estimate less than 25% cannot be justified based on the increased long-term yield of the stock. Assembly of a prospective life-table for the central subpopulation of the northern anchovy (*Engraulis mordax*) allows the discussion of intrapopulation and environmental controls on growth of the population. Using reasonable values for survival and growth in the embryonic, larval, and juvenile stages in the context of a life-table allows one to evaluate the stages where recruitment is controlled. From this manipulation it appears that significant decreases in recruitment could originate at any stage but marked increases in recruitment are only likely to arise from lower mortality rates in the embryonic and larval stages. The late larval stage of the anchovy could exhibit remarkable control on the level of recruitment through plasticity of the interaction between growth rate and survival. Maximum cohort biomass of the anchovy occurs late in the first year of life but current measures of juvenile survival and biological production are inadequate to explore density-dependent survival and growth rates.

La prise globale de poissons marins a été stable au cours de la dernière décennie mais le pourcentage de clupéidés est passé de la moitié au tiers de ce total. Ce déclin semble être causé par des variations du succès du recrutement quand la pression par pêche est élevée. Les modèles théoriques de population et les indices environnementaux corrélatifs ne permettent pas encore de fixer les limites des prises. Pour quelque temps, la quantification directe de la biomasse actuelle semble nécessaire pour l'établissement des contingents de clupéidés. Des études sur la précision et les coûts des estimations de la biomasse, à l'aide des méthodes actuelles, indiquent qu'on ne peut justifier un écart-type de l'estimation inférieur à 25% en fonction du rendement accru du stock à long terme. L'ébauche d'une table de survie éventuelle pour la sous-population d'anchois du Pacifique (*Engraulis mordax*) permet une discussion des contrôles environnementaux et intra-population sur la croissance de la population. En utilisant des valeurs raisonnables concernant la survie et la croissance chez les stades embryonnaires, larvaires et juvéniles, dans le contexte d'une table de survie, on peut évaluer les stades où le recrutement est contrôlé. D'après cette manipulation, il semble que les baisses importantes du recrutement peuvent se produire à n'importe quel stade, mais que les accroissements marqués du recrutement ne proviendront probablement que de faibles taux de mortalité aux stades embryonnaires et larvaires. À cause de la plasticité de l'interaction entre le taux de croissance et la survie, le stade larvaire avancé de l'anchois pourrait exercer un contrôle frappant sur le niveau de recrutement. La biomasse maximale de la cohorte chez l'anchois a lieu vers la fin de la première année de vie. Toutefois, les quantifications actuelles de la survie des juvéniles et de la production biologique ne permettent pas d'étudier la survie reliée à la densité ni les taux de croissance.

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Marine fish catch has been stable over the past decade at 45 million tons per annum but the clupeoid contribution has declined from one-half to one-third the marine fish catch (Anonymous 1981a). This has occurred through a chronic decline of herring catch and a drastic decline of the anchovy catches partly moderated by a recovery of sardine fisheries (Anonymous 1981a). In 1980, clupeoids represented 80% of the meal and oil fishery products, about 15% of the canned and cured fish, and 7% of the fresh or frozen fish (Anonymous 1981b). The major genera in the commercial fishery are the pilchard or sardine (*Sardinops* spp. and *Sardina pilchardus*, 7 million metric tons (t)), the anchovy (*Engraulis* spp., 3 million t), the oil sardine (*Sardinella* spp., 2 million t), and the herring, menhaden, sprats, and thread herring (*Clupea* spp., *Brevoortia* spp., *Sprattus* spp., *Opisthonema* spp., at 1 million t per genus per year). Fisheries are conducted on all ages and sizes of the clupeoids, and variations in recruitment have immediate effects on the fishery. In the past 30 yr the anchovy catch has ranged between one half and 15 million

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[1] This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

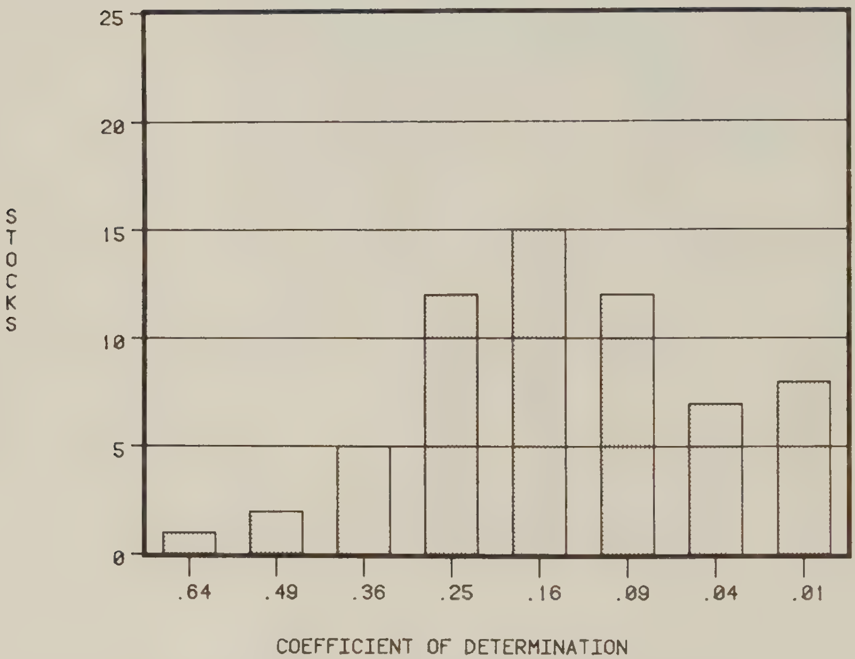

FIG. 1. Frequency distribution of indices of density dependence based on Tanner (1966). The coefficient of determination is the square of the correlation coefficient of the population growth rate versus the population size. All 62 values differ significantly from unity.

$t \cdot yr^{-1}$, sardine has varied between 1 and 7 million $t \cdot yr^{-1}$, and herring from 1 to 5 million $t \cdot yr^{-1}$. Most of this variation has been caused by changes in recruitment success during heavy fishing pressure.

Ten years have passed since Parrish (1973) stated at the Aarhus Symposium on Fish Stocks and Recruitment "... in most species for which detailed information is available, these (population regulation) factors operate mainly during the early stages of development (i.e. between the egg and the end of the first year of life) so that year-class strength is determined and population control mechanisms for most fish stocks operate before the individuals enter the exploited phase."

Improvement of the long-term management of clupeoids stocks will include (1) specialized studies on population size and environmental controls of reproductive success and (2) implementation of measurement and prediction procedures for controlling the impact of fishing pressure on clupeoid stocks.

The theory and application of population modeling does not appear to have much immediate promise for management of clupeoid stocks. A good example of the inadequacy of "density-dependent" controls on population growth is reported by Tanner (1966). Figure 1 is a summary of 111 time series of the relative amount of population change controlled by population size. In the 62 population time series where density and population growth were significantly negatively correlated, the degree of control was very low. Essentially, only 16% of the population growth was controlled by population size. More recently, MacCall (1980a) deduced that as little as 10% of the variation in mortality rate in the northern anchovy (*Engraulis mordax*) could be attributed to density-dependent causes.

Garrod and Colebrook (1978) have presented a large correlation matrix for 22 yr (1950–71) of recruitment of 18 North Atlantic stocks. If large-scale environmental features were a dominant influence on recruitment, independent of stock size and density, one would expect three modes: a positive mode would arise from stock pairs whose recruitment is favored by the same environmental features (i.e. positively correlated recruitment), a negative mode would arise from pairs of stocks in which an environmental change would simultaneously increase the recruitment of one stock and decrease recruitment of the other, and a central mode would arise from indifference of stock pairs' recruitment to general environment.

Figure 2 is a frequency diagram of the 153 stock pairs coefficient of determination (r^2). Coefficients of determination arising from negative correlations are separated from those arising from positive correlations. If one assumes no serial coherence with this length of time series, P = values of r^2 in excess of 0.25 ($0.05 < t < 0.01$) is strong evidence of association in the statistical sense that such a value would not likely arise by chance; however, a coefficient of determination as low as 0.25 on the interannual scale would have very little use in fisheries management or biological oceanography. More than two thirds of the pairs were positively correlated. This implies that certain general features of the environment such as lethal temperatures, turbulent mixing, and productivity have a weak large-scale, long-term control on population success, irrespective of population reproductive size.

General population theory and wide-scale environmental measurements may never provide adequate (Fig. 1 and 2) information for generating periodic decisions necessary to restore

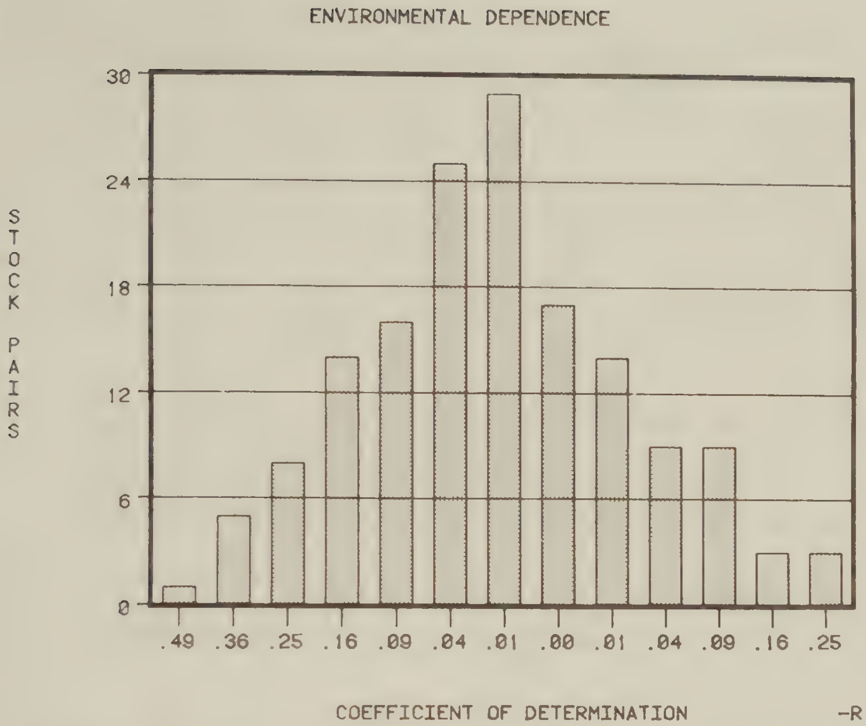

FIG. 2. An index of environmental dependence based on Garrod and Colebrook (1978). The coefficient of determination is the square of the correlation coefficient of all pairs of 18 North Atlantic stocks.

and sustain clupeoid fisheries. Until predictions of recruitment success are effective, management of clupeoids will depend on assessments of stock size and direct measures of recruitment. Gulland (1982) stated that "... the point in their lifespan (fishes) in which increased understanding would seem to be most rewarding is in the early life stages before recruitment ... The practical value of such an improvement in our scientific knowledge in terms of better management of the world's fish resources is considerable." It is the purpose of this paper to explore characteristics of the early life stages of the northern anchovy and the practical value of new procedures for restoration and management of clupeoid fish stocks.

Mechanisms of Population Control

The habitats of clupeoids are not known in sufficient detail to decide for any species what mechanisms other than fishing control reproductive success, population size, and potential fishery yield. The sheer logistics of mounting population/habitat studies with sufficient geographic scale, spatial intensity, and temporal continuity and competent samplers have so far prevented adequate explanations of annual fluctuations of clupeoid reproductive success. For convenience, most work on the stock-recruitment problem has had to accompany stock assessment activities. Similarly, most analytical work has been concentrated on the commercial sizes and planktonic stages. The result is that time series data are too simple and the occasional experimental approaches are too short-term to provide adequate information on the basis of recruitment overfishing in clupeoids.

I shall defer to the second section how early and how precise a recruitment prediction must be to be worth the cost of producing the estimate. For the purpose of this section I will assume that timely knowledge of recruitment success will be valuable for effective tactical management of clupeoids and some knowledge of recruitment variability will encourage strategic approaches to the limitation of overall fishing effort and associated capital facilities.

This section contains a prospective life-table of the northern anchovy central subpopulation. This is intended to focus the discussion in the subsequent elements of this section on where the life-cycle and in what manner the density-dependent and environmental mechanisms serve to control population size in *E. mordax*. The second element is a description of some density-dependent mechanisms. Lastly, environmental mechanisms are discussed.

General Features of an Anchovy Population

Vulnerability to predation and starvation changes so radically during the life cycle of a clupeoid that it is useful to erect a life-table as a guide to stages in which population size control by intrapopulation or environmental means may be effected. It is the purpose of this section on the population characteristics of the central subpopulation of the northern anchovy to describe the entire life cycle. While we have detailed knowledge of only the adult and planktonic stages (Smith and Lasker 1978), we can deduce the intermediate parameters for a first approximation. This is accomplished by the artifice of a stationary population model. New estimates of fecundity and growth (Hunter and Leong 1981; Mallicoate and Parrish 1981) for this subpopulation can be used with estimates of embryonic mortality (Picquelle and Hewitt 1983) and larval growth (Methot and

TABLE 1. Estimated and postulated life history characteristics for the central subpopulation of the northern anchovy (sources in parentheses).[a]

Category	Length (mm)	Mortality rate (daily)	Growth rate ($mm \cdot d^{-1}$)	Age (d)	Initial dry wt (g)	Initial number	Principal food	Principal predators
Embryo	Egg–4	0.25 (1)	—	0–7	3×10^{-5} (6)	3.50×10^{15}	Yolk	Filtering, biting (9, 10, 11, 12)
Early larva	4–10	0.16 (3)	0.5 (4)	8–19	2×10^{-5} (7)	4.74×10^{14}	Dinoflagellates, nauplii (8)	Biting
Late larva	10–35	0.05	0.325 (4)	20–96	5×10^{-4} (6)	6.94×10^{13}	Microcrustacea (6)	Fish, birds
Early juvenile	35–60	0.02	0.5 (4)	97–146	5×10^{-2} (6)	1.48×10^{12}	Microcrustacea, diatoms (4)	Fish, birds, marine mammals
Late juvenile	60–85	0.01	0.35	147–217	3×10^{-1}	5.44×10^{11}	Copepods, diatoms (4)	Fish, birds, marine mammals
Prerecruit	85–110	0.01	0.087	218–504	9×10^{-1} (7)	2.67×10^{11}	Copepods, diatoms (4)	Fish, birds, marine mammals
Early adult	110–135	0.0027 (2)	0.025 (5)	505–1504	2×10^{0} (7)	1.52×10^{10}	Copepods, euphausiids, diatoms	Fish, birds, marine mammals
Late adult	135–160	0.0027 (2)	0.02 (5)	1505–2754	4×10^{0} (7)	1.02×10^{9}	Copepods, euphausiids, diatoms	Fish, birds, marine mammals

[a] Sources: (1) Picquelle and Hewitt 1983, (2) Hanan 1980, (3) Hewitt 1982, (4) Methot 1981, (5) Mallicoate and Parrish 1981, (6) Hunter 1976, (7) Hunter and Leong 1981, (8) Lasker 1975, (9) Hunter and Kimbrell 1980, (10) Lillelund and Lasker 1971, (11) MacCall 1980b, (12) Theilacker and Lasker 1974.

Kramer 1979; Methot 1981) to postulate a total life cycle stationary model.

In Table 1 I have listed the assumed characteristics of the anchovy population. Citations for the properties for which we have any data are listed. These parameters or their range are known only for time periods we have been fortunate enough to observe. The primary utility of listing the known and assumed values is to direct the discussion below to a small number of specific characteristics of the population, and to speculate how these might be influenced by the population size and the environment within the first year.

For all but two of the stages, the population is divided into 25-mm length groups. The first two stages, the embryonic and early larval, are divided from each other on the basis of the onset of feeding: the transition to late larva is arbitrarily set at a length of 10 mm.

The fecundity schedule from which the initial number in Table 1 is derived is found in Table 2. In this instance the fecundity rate is controlled only by the number of batches of eggs per year and the number of eggs per batch at a fixed rate per adult gonad-free weight. I have assumed no weight- or age-specific change in the eggs produced per gram of female. We have no estimate of the variability of the number of batches per year but the batch fecundity appears to vary on the order of 20% on an interannual basis (Hewitt 1982). I also do not know whether the season of slower spawning is based on many females spawning at a slow rate or a few females spawning at the normal rate.

A schematic drawing of a cohort of northern anchovy is illustrated in Fig. 3. The mortality and biomass curves are distorted by the log–log plot of numbers and biomass on age in order to emphasize the role of the early stages. The biomass of the cohort undergoes four transitions, which may be instructional for the study of recruitment. Three of the changes occur in the larval stage and one in the juvenile stage. For the purpose of this discussion, I will first point out some functional anatomical features for each stage and follow with a simple model of their mortality and growth.

Embryo

The embryonic stage is characterized by rapid loss in weight per individual and rapid decline in numbers. As a relatively large member of the zooplankton, the egg is subject to passive filtration. It is also probably vulnerable to biting as the visual distortion of the clear egg, the increasing visual contrast, and later motions of the developing embryo heighten the detectability by mechanoreceptors and vision. The vulnerability may also be heightened at hatching as the protective integument of the egg is lost: clues for chemoreception by predators may also increase. Lillelund and Lasker (1971) described the mortality associated with chance contact of yolk-sac larvae with copepods even when no feeding by the copepods occurs. Theilacker and Lasker (1974) evaluated the predation by euphausiids on yolk-sac larvae. Also, there appear to be many malformed embryos in nature (E. Sandnop, Southwest Fisheries Center, pers. comm.; H. Santander, Instituto del Mar del Peru, Collao, Peru, pers. comm.; E. Stevens, Southwest Fisheries Center, pers. comm.) at all stages; some may live through the yolk-sac period but are too distorted for successful first feeding. The anchovy requires high food density at first feeding; layers (Lasker 1975) and horizontal patches of food (Vlymen 1977) are a condition for successful first feeding. The embryos are never very far from low lethal temperatures (Brewer 1976) in the water column (12°C at 50 m depth; Eber 1977). The adults appear to skirt lethally cold patches of newly upwelled water (Lasker et al. 1981), and embryonic mortality could be caused by lateral advection into those areas. Lastly, chronic and widespread colder-than-average water temperatures would retard develop-

TABLE 2. Life and fecundity table for the females of the central subpopulation of the northern anchovy.

Age (yr)	Number	Weight (g)[a]	Fecundity[b]				
			b	*f*	*n*	*N*	Cumulative
0	1.74×10^{15}	—	—	—	—	—	—
1	2.11×10^{10}	12.8	532	7	24 000	5.00×10^{14}	5.00×10^{14}
2	7.88×10^{9}	16.5	532	20	77 000	6.92×10^{14}	1.38×10^{15}
3	2.90×10^{9}	20.7	532	20	110 000	3.19×10^{14}	9.58×10^{14}
4	1.07×10^{9}	24.4	532	20	130 000	1.39×10^{14}	5.56×10^{14}
5	3.92×10^{8}	27.8	532	20	148 000	5.80×10^{13}	2.90×10^{14}
6	1.44×10^{8}	31.5	532	20	168 000	2.41×10^{13}	1.45×10^{14}
7	8.24×10^{7}	35.5	532	20	189 000	1.56×10^{13}	1.09×10^{14}
Sum						1.75×10^{15}	3.94×10^{15}
Mean generation time (yr)							2.25

[a] Grams wet weight for a representative female.

[b] b = batch fecundity in eggs per gram of female; f = frequency of batches per year; n = number of fertilized female eggs per female adult per year assuming 50:50 sex ratio; N = total number of fertilized female eggs spawned by all females of that age in a year; — = immature.

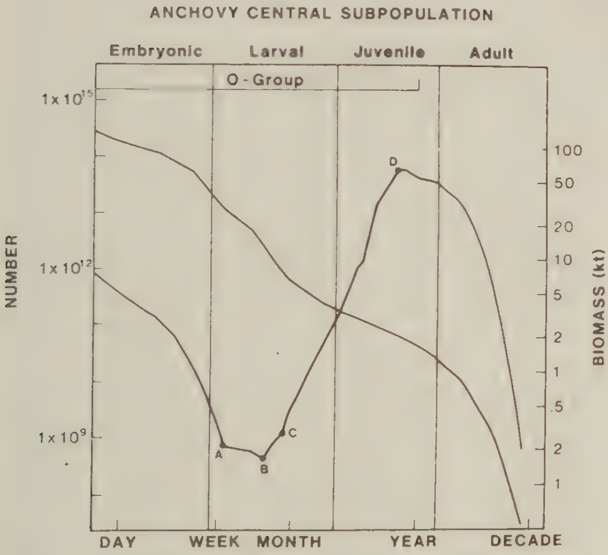

Fig. 3. Cohort estimates of number and biomass of northern anchovy central subpopulation. Values are based on a series of exponential mortality equations for each stage of the life cycle in approximate stationarity.

ment and prolong the highest mortality rate phase of the life cycle.

Larval period

In the larval period, the cohort biomass rate of decline is arrested at point A (Fig. 3) but the growth in weight of the individual larva is insufficient to balance weight loss of the cohort through mortality. At point B the cohort begins its net growth and this growth advances to a sustained high rate at point C. The break at point A may represent a radical change in vulnerability to filtration predation. At this length (5 mm) we see the first demonstrable change in day and night sampling with a 1-m net. Day–night differences in evasion are about 3:1 at this length (Smith 1981). O'Connell (1981) and Hunter and Coyne (1982) have described the onset of schooling and associated anatomical, sensory, and behavioral characteristics. By point B the larva has eye retractor muscles, red muscle and red blood corpuscles, and night vision. Plankton net capture of this stage (15 mm) is a rarity. Point C may represent the faster weight gain and lower mortality aided by the onset of metamorphosis into the adult form (Methot 1981; Hunter and Coyne 1982). The lateral line is formed, respiration is through gills rather than cutaneous, red muscles are in layers, the stomach is formed, and the degree of tolerance to starvation is greatly increased. Sustained high growth rate probably still requires the detection of highly aggregated food supplies (Lasker and Zweifel 1978; Vlymen 1977; Owen 1981).

Juvenile

The maximum biomass of the cohort is achieved at point D in Fig. 3. Methot (1981) pointed out that the elaboration of gill rakers in the juvenile may coincide with the maximum rate of coastal upwelling and diatom abundance (Tont 1981). Methot (1981) also briefly described the concentration of juveniles in the continental borderland. Since the juvenile stage is at a maximum point of biomass and appears to be concentrated in a small fraction of the adult habitat, this would appear to be an extremely vulnerable point for the recruitment to the population by either density or environmentally mediated controls on population growth.

In this simple model, the life cycle is controlled by three factors in each stage. The first factor is the initial number that originates from the previous stage. The second factor is duration or the reciprocal of daily growth rate. The third factor is instantaneous mortality. In Fig. 4, these three factors are illustrated. The contrast of the mortality rate and duration of the early stages may be emphasized by comparison with the nearly horizontal curve of adult mortality. Since these curves are based on stationarity, any combination of increased stage-specific mortality that intersects the adult line will lead to a recruitment below the replacement value. To evaluate the importance of these parameters, it will be convenient to perturb each parameter for each stage.

Mortality

In Table 3, the parameters controlling the hypothetical O-group of the northern anchovy have each been perturbed

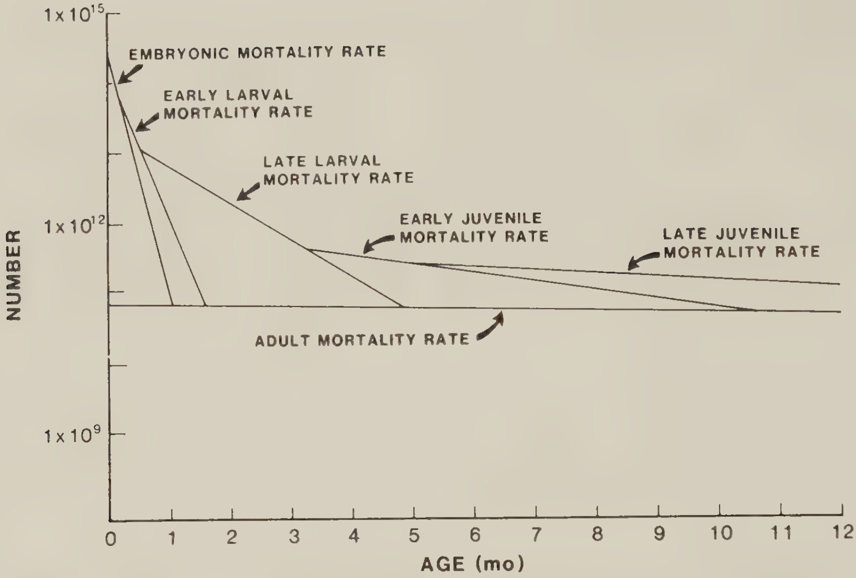

FIG. 4. A diagram of the O-group mortality curves to compare the joint effects of stage duration and stage mortality rate on the resulting adult population of northern anchovy central subpopulation.

sufficiently to effect a fivefold decrease or increase in the level of recruitment. It should be remembered at this point that we do not know if the values we have estimated for parameters so far are central in an interannual sense. The early larval mortality parameter is probably the best known on an interannual scale. The value 0.16 is the mean of 21 annual values in the period between 1951 and 1979. The range is 0.03 and 0.24, and Hewitt (1982) found that the higher values of mortality are associated with higher rates of larval production and wider distribution of the spawn. Interannual variability in embryonic mortality for the brief period between 1979 and 1983 has also been large, with estimated rates ranging from 0.00 and 0.41 in five estimates.

It is interesting to note that no manipulation of the juvenile mortality rates over a period encompassing 4 mo and 50 mm growth in length will result in a fivefold increase in the number of recruits. All the other values for mortality appear reasonable.

Duration

When one deals with duration of the stage or growth rate, it is also seen that a fivefold increase in recruitment cannot solely originate in modification of the juvenile periods' values. At the embryonic stage, the duration is controlled by temperature alone and the parameter requiring that this stage be completed in 1.6 d is not reasonable; thus, a fivefold increase in recruitment does not appear to be a reasonable outcome in this stage alone. The temperature required to lengthen this stage to 14.5 d is nearly lethal as well (Zweifel and Lasker 1976). The observed variations in growth rate in recent years would not support the idea of plasticity to the necessary extent to change the recruitment fivefold (Methot 1981), and field-measured durations of this stage are not distinguishable from the same value measured in laboratory conditions. The late larvae parameter values are as reasonable at both extremes of duration as they are in mortality.

The juvenile and prerecruit duration parameters still retain sufficient plasticity to permit fivefold decreases in recruitment but the only source of a fivefold increase would be the sustained growth at $0.2\ \mathrm{mm \cdot d^{-1}}$ for more than 4 mo. The observations necessary to evaluate this are not yet documented.

Adult

We see in Table 2 that the mean generation time is over 2 yr; thus, a fully functional model of this population would require that adjacent years of recruitment be assembled into the resultant adult portion of the population with its own growth, mortality, and fecundity rates. This is beyond the scope of this paper, but it is worthwhile to note that adult mortality rates of the small clupeoid species may well vary significantly. R. D. Methot (pers. comm.) has observed this phenomenon in the northern anchovy. The number of eggs per batch per gram of female appears to vary on the order of a few tens of percent (Hunter and Leong 1981) rather than the fivefold discussed for the other population-controlling parameters. The number of batches per year could well be quite changeable. From the seasonality of the larval production over the past 30 yr (Hewitt 1982), the northern anchovy would not likely vary more than two- or three-fold in the annual rate of fecundity. More directed study on seasonality of adult reproductive behavior is required.

Some Density-Dependent Mechanisms

Some unusual circumstances of density dependence in the northern anchovy are caused by the fact that all but 30 d of a 5-yr life cycle is spent in schools (Hewitt 1981; Hunter and Coyne 1982) and the schools are often found aggregated into school groups (Fiedler 1977). This means that the more obvious forms of competition for food and space appear to be compromised by aggregation behavior. The following section contains comments on competition, cannibalism, and the stimulation of aggregation and growth of predator populations.

Competition

The dimensions of anchovy schools are of the order of tens to hundreds of metres, with most schools in the lower range, and possibly half of the fish are in the few schools more than 90 m in

TABLE 3. Parameter[a] changes leading to a fivefold decrease or increase in recruitment for the central subpopulation of the northern anchovy. Experimental values underlined (see Table 1 for references).

Stage	Instantaneous mortality (daily)	Stage duration (d)	Growth rate ($mm \cdot d^{-1}$)
Embryo			
Stationary	0.250	8	—
1/5	0.454	14.5	—
5×	0.048	1.6[b]	—
Early larva			
Stationary	0.160	12	0.500
1/5	0.297	22.2	0.270
5×	0.026	1.9[b]	3.158[b]
Late larva			
Stationary	0.050	77	0.325
1/5	0.072	110	0.227
5×	0.029	44.5	0.559
Early juvenile			
Stationary	0.020	50	0.500
1/5	0.053	131	0.190
5×	Inf.[b]	Inf.[b]	Inf.[b]
Late juvenile			
Stationary	0.010	71	0.350
1/5	0.033	232	0.108
5×	Inf.[b]	Inf.[b]	Inf.[b]
Prerecruit			
Stationary	0.010	287	0.087
1/5	0.016	449	0.056
5×	0.0044	126	0.200

[a] Parameters in the equation $NT(I-1)\exp[-Z(I)T(I)]$ where $NT(I-1)$ is the number at the beginning of interval I, Z is the instantaneous rate of mortality, T is the time in days, and $NT(0)$ is the annual fecundity (both sexes).

[b] Unreasonable values or Inf. (infinity).

diameter. The maximum observed size of a school is about 400 m (Mais 1974). A common density within a school is $15\ kg \cdot m^{-2}$ (Hewitt et al. 1976). When one considers a single school (Smith 1978) the food available in the water column would be the accumulated excess of production over consumption for the interval since the last school occupied that area. Anchovy schools at any instant occupy less than 1% of their habitat (Smith 1981) but the chances of reencountering an area or encountering an area already fed upon by another school is relatively high for time periods of weeks. All these events together might cause the schools or school groups to move apart where production of food was inadequate, whereas schools might congregate in areas where food production exceeds consumption. At some population size for anchovy, or at some joint biomass of all the plankton-feeding members of a coastal pelagic guild, competition could occur between schools or among school groups.

Competition could occur between adults and juveniles if the adults deploy over a wide area for feeding when productivity is high and reassemble on the brood habitat with the juveniles at the approach of spawning time. By that time, the juveniles are nearly a year old and their food requirements are the same as the adults. The juveniles will have invested most of their energy intake into growth in length and will have relatively less fat than the adults. The outcome, limiting to the population growth rate, might be to delay the onset of spawning by the O-group and lessen the number or repetitive batches spawned by adults.

There is evidence that all or most juveniles go through a coastal phase (Methot 1981) in water less than 90 m (50 fathoms) deep. In the major brood area for the northern anchovy the mainland coast contains 17% and the coastal islands contain 7% of the 25 000 km^2 brood area. Based on capture rate the shallow waters contained at least 70% of the juveniles. Thus, while a habitat calculation based on Fig. 3 might show food to be sufficient, intraspecific food-limited growth could be a factor for juveniles at large population sizes.

Competition is not likely to be a factor in the early larvae of northern anchovy. Growth rates in the sea are similar to those in the laboratory under rich feeding conditions (Methot 1981).

In summary, competition for food is not likely to be a consideration for early larvae. Competition for food should be considered for late larvae (Cushing 1983).

Competition, if any, for juveniles in a cohort may be exaggerated if most of the juveniles must pass through a small, shallow coastal segment of their habitat. Competition between the adult and juvenile segments of the population could be intense at the winter zooplankton and phytoplankton minimum when the adults assemble on the brood grounds at spawning time. Lastly, competition among adults is likely to be between schools that occupy their local habitat intensely and may reoccupy it frequently.

Cannibalism

Cannibalism is a potential density-dependent, population-limiting mechanism for the northern anchovy. Depending on the population size, cannibalism could be important as incidental to filter feeding, it could be accentuated by directed filtering on high egg concentrations, or by switching from biting to filtering behavior.

If schools must perpetually move to support their high food requirement, the population cannibalism would merely entail a school encountering the patch of eggs deposited by it or another school. From the distribution of fish schools I would expect the reencounter of a patch of eggs by the school that spawned it to be a constant probability at all population sizes or a decreasing probability with increased population size. The encounter and incidental filtration of embryos by a different school (than that which spawned it) would be an increasing function of population size.

Eggs of anchovy disperse after being spawned. Hunter and Dorr (1982) found that filtering anchovy would filter selectively in anchovy egg concentrations of $1 \cdot L^{-1}$ or more. This raises the possibility that rather than incidental cannibalism, at certain population levels directed filtration could represent an important shift in the impact of egg cannibalism on the population growth rate.

A third density-dependent mechanism would be switching from biting to filtering at high population sizes. If the preferred food at low anchovy population sizes were herbivorous crustaceans obtained by biting, the probability of egg cannibalism would be low. If the population size actually decreased the population sizes of herbivores, the additional phytoplankton production and the shortage of crustaceans could increase the incidence of filtering to the extent that population growth rate would be controlled.

Brief observations of cannibalism in the northern and Peruvian anchovy (Hunter and Kimbrell 1980; MacCall 1980b;

Santander et al. 1983) indicate that under current population sizes (very low for both stocks), cannibalism is responsible for a relatively small fraction of the mortality of the spawn. If cannibalism becomes an important regulator of the population growth rate it could occur by (1) directed filtering on dense aggregations of eggs, (2) encounter of other schools' patches of eggs, and (3) the anchovy population switching from biting to filtering feeding behavior.

Aggregation and growth of predator populations

The rapid development, mortality, and dispersal of embryos and larvae of the anchovy would make less likely the aggregation and growth of populations that prey on these stages. There is evidence for reproductive success of coastal birds changing in response to juvenile anchovies. It seems likely that populations of marine mammals and fishes could respond to adult anchovies as well. Anderson et al. (1982) described the improved rates of survival of young of the endangered brown pelican population. Should that success continue, the pelican could in turn begin to exercise control of the juvenile survival rate, particularly if most juveniles must pass through the nearshore region, as postulated by Methot (1981).

Scale deposition rates (Soutar and Isaacs 1974) of the major temperate fish stocks were collectively 3 to 5 times greater at the turn of the century (Smith 1978). This coincides with a population minimum of the northern fur seal harvest in 1911, which has been accompanied by a resurgence of the fur seal population and a concomitant decrease in the scale deposition rate (Anonymous 1977, p. 242). The current fur seal population consumes about 1 million t of pelagic fish per year in the Northeast Pacific (Lander and Kajimura 1982). If the high populations of the early part of this century stimulated the growth of the predatory populations this could be an important form of density-dependent control of the anchovy population.

Some recent years of poor recruitment per spawner in the northern anchovy have also been years of unusual Pacific mackerel (*Scomber japonicus*) abundance on the brood grounds (R. D. Methot, pers. comm.). To the degree that the mackerel aggregates on the schooled anchovy juveniles, this could be considered an important density-dependent factor in the regulation of the anchovy population. A second phase of this interaction would be if the mackerel population increases in later years as a result of the abundance of anchovy.

Thus we see that marine birds, mammals, and fishes could establish and control growth rates for a clupeoid fish population such as the anchovy. Only in the case of the guanay off Peru (Tovar 1983) and pelican feeding on anchovy juveniles (Anderson et al. 1982) have sufficient data been collected to establish a convincing link to anchovy population control by the mechanism of aggregating or stimulating the population growth of a predator population.

Environmental Mechanisms

The high-seas support no clupeoid stocks in the temperate zone. Usually in the study of the environment of clupeoid stocks we are examining the interaction of the open-sea environment in juxtaposition with the coastal and neritic ones which comprise the clupeoid habitat. The definition and interpretation of these zones must be done with care as exemplified by the writings of Bakun and Parrish (1982), Bernal and McGowan (1981), Chelton (1982), Chelton et al. (1982), Colebrook (1977), Hewitt and Method (1982), Lasker et al. (1981), Owen (1980), Parrish and MacCall (1978), and Smith and Eppley (1982). The mechanism invoked must match the spatial, temporal, and other biological characteristics of the species for which population control is implied. For example, the California Current exhibits laminae of epipelagic fishes in which the clupeoid pair, sardine and anchovy, occupy intermediate areas; onshore are the speciose rockfishes and abundant flatfishes aligned to the bathymetric features of the coast and their interaction with the passing currents. Offshore of the clupeoid pair are the oceanic species of pelagic schooling fish, the jack mackerel (*Trachurus symmetricus*) and the saury (*Cololabis saira*) (Loeb et al. 1983). These are widespread over the transition zone of the Northeast Pacific.

The mechanisms to be discussed below are (1) lethal conditions, (2) biological production, (3) changes in the biological community, and (4) physical and chemical changes in the habitat. Many of the mechanisms to be discussed differ from density-dependent mechanisms only in that the decrease in population growth rate is incidental to the environmental change rather than being a direct result of the interaction of population density and the carrying capacity of the environment.

Lethal temperature, oxygen, etc.

A relatively large fraction of the sardine eggs spawned were placed in sites where the temperature at 10 m of depth (13°C) is known to be lethal to embryonic stages before first-feeding can occur. In 1953, lethal (Ahlstrom 1965) temperatures swept the major spawning grounds of the northern subpopulation of the Pacific sardine (*Sardinops sagax*) and no spawning was detected there. After the warming trend in 1958, virtually all sardine spawning was located in the southern California bight where spawning had previously been excluded. It may be seen that density-independent controls of stock size may be more restrictive to the spawning grounds than the feeding grounds; thus, studies of these features will have to be carefully placed in time and space and be adaptively conducted to estimate the population effect.

Biological production

Based on the early work of Murphy (1966) and Ryther et al. (1971) and later writings by Walsh (1981) and Smith and Eppley (1982), it seems plausible that stocks of clupeoids could achieve sufficient biomass to approach the limits of productivity. Neither the current measures of fish biomass, fish food requirements, nor biological production are adequate to test this hypothesis because the interaction of the disappearance of food and the increased energy of searching for the remainder cannot be studied until a clupeoid population is found whose density is near the carrying capacity. Since the clupeoid populations constitute a significant nitrogen source, the primary limitation on production would be the time between the renitrification of the environment and the elaboration of plankton edible by the clupeoid stock involved. The poleward and offshore migrations of the temperate clupeoids might reflect a behavior brought about by limitations of biological production and the relative standing stocks of food (Lasker 1970) in the two environments. Excellent measures of recruitment would be necessary for detecting subtle effects of limits of biological production; given the mobility of the juveniles at maximum cohort biomass, recruitment failure studies would require intensive regional measures of feeding and food availability.

Biological production is not yet measured routinely over oceanic areas of significant size relative to the distribution of clupeoids. For the most part, secondary production is unmeasureable by present techniques, and the elaborate methods necessary to estimate primary production in a broad geographic area have defeated attempts to obtain a seasonally and geographically satisfying estimate of primary production in any upwelling coastal area. Eppley et al. (1979) reported the primary production in a small area of the Southern California Bight and Smith and Eppley (1982) compared the time series with that of the northern anchovy biomass in that small area. The main barriers to temporally and spatially coherent measures of primary production are that the primary production will likely be very patchy in space and episodic in time (Tont 1976).

There are some data with which to form plans for studies of primary and secondary production off California. Colebrook (1977) analyzed the CalCOFI biomass data and found a clear pattern for the major elements of the biota. He found that there were two clear planes of variability: one was associated primarily with the California Current and the other was cross-shore near the coast. The organisms associated with the subarctic flow from the transition zone were in the "functional groups" Thaliacea, Siphonophora, and Medusae. Organisms whose orientation was primarily cross-shore were in the functional groups Copepoda, Euphausiacea, and Chaetognatha. Another description of the same data may be found in Fleminger et al. (1974); they described the coastal upwelling as extending the habitats of the temperate ocean toward the tropics adjacent to the coast in a narrow band.

Similarly, in a phytoplankton community study, Malone (1971) described a geographic division oriented to the coast. In the vast majority of the oceanic area and most of the time that the nannoplankton did not dominate was during episodes of coastal upwelling; at that time the production was primarily by large diatoms. Malone found that the geography of the bloom could be described by the presence of chlorophyll *a* greater than $0.5\ \mathrm{mg \cdot m^{-3}}$ at the surface. Long time-series of episodic diatom blooms were described by Tont (1981), and the nature of the episodes was described by Tont (1976). Tont found that most of the diatom biomass was detected in three blooms per year and the duration of the upwelling effect was slightly more than 1 mo.

Given these diagnostic features of primary production, the spatial and temporal description of interannual change should be approximated usefully by ships under cloud cover and by satellites when conditions are favorable. Smith and Eppley (1982) found that statistical relationships among the levels of production were exponential. That is, the relationship among primary production, zooplankton volume, and anchovy larval abundance was highly nonlinear. Larval growth and survival and recruitment should be compared with simple indices of the area influenced by upwelling. Alvariño (1980) has already begun the characterization of the spawning habitat in terms of the invertebrate communities there and in nonspawning areas.

Walsh (1981) illustrated the problem with biological productivity measurements by reporting a "time-series" of primary production with a range of 1966 to 1978 off the coast of Peru. He stated that the 1966 values are high because they were taken in a high chlorophyll area at the shelf break and that the 1976–77 data are low because repeated time-series stations were taken within a low chlorophyll area near the coast. This means that 101 of 185 stations are not representative. He failed to mention in the text, but listed in tables, the fact that 149 of the 185 samples reported were taken at 15° south in an area where Santander (1981) showed that there are usually few anchovies. Also, 159 of the 185 samples reported were from February through May and only 4 samples were during the austral winter in August and September. Walsh also chose to calculate an overall average from cruises or citations that varied in number of samples from 4 to 43. Thus, we see that someone constructing a model that includes primary production off Peru is forced to use an invalid set of samples. The average rate of carbon fixation was $3.98\ \mathrm{g\,C \cdot m^{-2} \cdot d^{-1}}$. The situation is little better off California where there are many measurements within 30 km of the coast, and 1 yr of primary productivity reported (Owen 1974) with 38 stations spread over 12 mo and 250000 square nautical miles (M^2). Of these, only three were in the habitat of the central subpopulation of the northern anchovy in February–March of 1969, one station in May–June, two stations in August–September, and two stations in November–December.

It would appear from this that it may be some time before a primary production time-series of sufficient extent, coherence, and duration is availalable with which to consider a fundamental property of eastern boundary currents, the habitat of massive clupeoid populations.

Changes in the biological community

Loeb et al. (1983) described the large-scale spatial relationships of the organisms constituting the community that normally contains the schooling pelagic clupeoids, anchovy and sardine, delineating also the offshore, inshore, subarctic, and subtropical boundaries of this community. One may see from the time-series work of Bernal and McGowan (1981) that the relative size of these zones and the clupeoid habitat off California may be quite changeable. Colebrook (1977) estimated that the subarctic boundary and strength of the California Current parallel to the coast was the most important influence on biota and that a second significant plane of variability existed onshore and offshore.

There is frequently little distinction between those changes in the biological community that are brought about by the population in question and those that are merely incidental to other environment changes. For example, if the anchovy stimulated the aggregation and growth of predatory populations in its habitat and these populations grew to control the anchovy, the incidental effect on the cohabitant sardine might well be determined to be density independent. Thus, it is the origin of the change rather than the effect of the change that distinguishes between these phenomena and those described above.

Physical and chemical changes in the habitat

Advection — Chelton et al. (1982) concluded that large-scale variations in the flow of the California Current play the dominant role in controlling zooplankton biomass by advection of nutrients. Their argument is strongly supported by the coherent response of the zooplankton volume over a very large oceanic area (240 × 1000 M) to changes in flow between 1955 and 1959, and supported by the rest of the time-series between 1951 and 1979. Murphy (1966) in his study of the sardine population noted that the annual rate of flow into the habitat was $47 \times 10^{12}\ \mathrm{m^3 \cdot yr^{-1}}$ and that the zooplankton transported in was $0.6\ \mathrm{g \cdot m^{-3}}$ and that transported out of the California Current region was $0.05\ \mathrm{g \cdot m^{-3}}$. He estimated that the imported zooplankton was equal to one standing crop but acknowledged that the species composition was different. Transport over most of the area is simple but a narrow band near the coast is complex (Hickey 1979), and one would need to know the orientation of various phytoplankton, zooplankton, and fish species to these general areas to interpret these results more fully. Haury and Shulenberger (1982) were unable to confirm the nutrient transport hypothesis of Chelton et al. (1982).

Wind-stress curl — Chelton (1982) used the wind-stress curl data assembled and reported by Nelson (1977) to describe a mechanism for the addition of nutrients to the euphotic zone by upwelling in a zone about 60 M offshore.This effect would extend between San Francisco and northern Baja California. No time-series or source water analyses are yet available to evaluate the range of this phenomenon or its effect on zooplankton and pelagic schooling fishes.

Isopycnal shoaling — Isopycnal shoaling is a large-scale effect caused by geostrophic tilting of isopycnals (uplift of entire density structure at coastal margin of gyres). As these isopycnals are inserted into the euphotic zone, productivity is enhanced. When the long-term, large-scale time-series of salinity (Chelton et al. 1982) is compared with advection, it appears that neither horizontal nor vertical advection is dominant for nutrient addition to the California Current. They emphasized that the vertical motion is not due to classical wind-induced coastal upwelling but is associated with geostrophic tilting of isopycnals from large-scale, low-frequency changes in the transport; thus, both horizontal and some vertical advection are caused by the flow of the California Current.

Wind-driven coastal upwelling — Barber and Smith (1980) characterized coastal upwelling ecosystems by several quantifiable features: (1) midwater oxygen minimum layers, (2) highly organic sediments, (3) anoxia, (4) denitrification and hydrogen sulfide events in subsurface waters, (5) large bird populations, and (6) guano deposits.

Source water — The physical introduction of deeper water into the euphotic zone, whether by isopycnal shoaling, coastal wind-driven upwelling, or wind-stress curl, generally has the effect of cooling and adding nutrients. The exceptions are, of course, when the source water is itself warm or nutrient free. Barber and Chavez (1983) emphasized the relationship of the qualities of the source water for upwelling to the response of the euphotic zone.

Since the California upwelling zone is not well defined or as extreme as the criteria established by Barber and Smith (1980), it will be useful to organize some measures that can be estimated from a variety of platforms in addition to the standard surveys. Surface chorophyll *a* in the range 0.5–10 mg·m^{-3} should be a useful boundary feature. Copepod biomass above 10 g·1000 m^{-3} in the upper 140 m and euphausiid biomass over 2·1000 m^{-3} in the upper 140 m should also serve as ready guides to the outer limit of the upwelling impact zone. Since these macroplankton have taken several weeks (copepods) or months (euphusiids) to respond to the upwelling enrichment, one should not expect these values at the site of upwelling.

Why is the recruitment to the central subpopulation of the northern anchovy so variable? To echo Gulland's (1982) theoretical paper, "Why is the recruitment to the central subpopulation of the northern anchovy not so variable?" At the beginning of the Mechanisms of Population Control section, we posed an extremely simple model of eight arbitrary stages in the anchovy life cycle. Following the lead of Shepard and Cushing (1980), the controlling parameters of each stage were the mortality and growth rates (Murphy 1961) of a stage of fixed length interval. The obvious reason why recruitment can vary is that relatively minor changes in these exponents can singly change the outcome severalfold. If these parameters are correlated with each other in a cohort, their joint effects would be devastating. If the later fate of the cohort is ultimately controlled by the carrying capacity of the environment, some of the early life stage losses or gains could be nullified. If the growth rate and the mortality rate were each adjusted independently and stochastically on a weekly basis, there would be a strong temporal averaging process. Similarly, if weekly cohorts encountered radically different conditions, there would be a second temporal averaging process. Thirdly, if the environment with respect to growth and mortality rate were structured as a mosaic, each sector of which had different rates, there would be yet another averaging process. Thus, we see that the answer to the question of why recruitment is constant is that temporal averaging within each cohort, temporal averaging among cohorts, and spatial averaging all taken together would likely enforce a certain level of stability on the eventual population size. Given the expense of confirming theory, development of predictions, and establishing monitoring systems with which to implement management recommendations (for stocks distributed over thousands of square kilometres of coastal ocean) the practical questions of costs must be raised. This is the subject of the next section.

Evaluations and Predictions

Thirty years ago, the chief problem in clupeoid fisheries was to define the stocks that had not yet been fished. Most of the catch of clupeoids in the past three decades was from stocks that had not yet been evaluated at the beginning of that period. While there are still isolated stocks of clupeoids that have not been fished, their potential yield appears small relative to those stocks that have been fished. Thus, with regard to the biological and economic yield from this taxonomic group, the largest remaining unexploited resource is effective stock management.

The physical yield from the clupeoid stocks may be expected to follow rather simple (Blaxter and Hunter 1982) (even if elaborate in total) biological rules for reproduction and harvest in a varying environment. The economic yield will probably be dominated for some years by increasing values caused by the increase of the human population and the conversion of the catch from relatively low value products of fish meal and oil to higher valued canned and cured products. Restoration of the stocks under the condition of higher demands and higher values is a first management priority. Higher stocks may be expected to yield more for less fishing effort, recover from natural variations faster, and provide other values as forage for coastal birds and migratory predators such as marine mammals and larger fishes.

Clupeoid O-Group Biological and Economic Models

Lenarz (1971) explored some economic consequences of management of the recovery of the Pacific sardine stock and the subsequent long-term yield as a function of the precision of management advice. Characteristics of sardine recruitment elucidated by Murphy (1966) were incorporated into the model. These were the reproductive capacity, recruitment variability, and the tendency for annual recruitment success to be linked with the previous years' recruitments, namely that recruitment failures tended to occur in runs, as did successes. He explored the management tools, quota, and fishery closure. Above a fixed biomass level fishing mortality was controlled and below that level the fishery was closed.

The simulation by Lenarz (1971) did not consider the economic effects of the yield but explored long-term average yield and yield per unit-of-effort as a function of management policy and the precision of estimates on which the policy was based. The policy of total closure at a fixed biomass increased the long-term yield about 1% but increased the yield per unit of fishing mortality by 0.4. Allowing the upper limit of fishing mortality to rise to 1.05 resulted in small long-term *gains* in average yield but significant *losses* in yield per unit of fishing effort. Precision management to maximize biological yield and yield per unit of fishing effort resulted in a closure of the fishery in 25% of the years for periods up to 4 yr. The quality of the biomass estimates had a moderate effect on yield and yield-per-effort when crude estimates were used, but 10% increases in yield and yield-per-effort resulted from improving the multiplicative error factor from 4 to 1.5.

Huppert et al (1980b) combined a biological model, a biomass-dependent yield-per-effort fishing model, and an economic yield model to explore the benefits of different management policies for the reduction segment of the northern anchovy fishery. They also included stochastic variability in actual recruitment and in the estimation of stock biomass. Their management policy included (among other things) a maximum on total catch and a closure of the fishery when the biomass was below set limits. Their management policy was based on a biomass estimate and they allowed the standard error of estimate to improve from 0.4 to 0.05 (about 2.5 to 1.05 on the Lenarz scale). The cost of the survey was scaled to the sampling effort and cost of a survey using 500 samples (1978 dollars). They assumed that survey costs were proportional to the number of samples and that the standard error of estimate decreased as the square root of the number of samples.

Huppert (1981, p. 73) concluded that the diminishing returns of value from the catch per unit of survey cost became negative between proportional assessment standard errors of 0.30 and 0.25. Further work of a similar nature was used to demonstrate the added value of allocating a portion of the catch based on the spawning biomass estimate and another portion at midyear based on a hypothetical recruitment estimate (Huppert et al. 1980a). They found that a very accurate and precise estimate of recruitment (0.1 standard error as a fraction of the mean) (Anonymous 1983) could augment the spawning biomass estimate usefully only if the annual cost of the recruitment survey was materially less than $\$250\,000 \cdot \mathrm{yr}^{-1}$. They did not explore the value of a recruitment survey without a spawning biomass survey.

The scale of the fishery in the work of Huppert et al. (1980a, 1980b) and Huppert (1981) is probably too small to apply directly to the fishery commodities of a global clupeoid fishery, but some dimensions would be interesting to expand to that scale. If we incorporate the data for the Lenarz (1971) model of the value of a sardine recovery and the data from Huppert et al. (1980a, 1980b) and Huppert (1981) for improving the precision of management, we should be able to project the management research and management tactical costs for restoring and sustaining global clupeoid yields.

The expected monetary value for an annual 400 000 t catch of northern anchovy (fished for reduction to meal and oil) is $4 million, or about $10 annually per metric ton of yield. Herring have yielded 3 million t for a long period, rose to nearly 5 million t for a brief period, and then fell to 1 million t currently. Anchovies have yielded 15 million t briefly and now yield 2.5 million t. Assuming that the combined restored catch could be approximately 10 million t, the restored values would be $75 million above the harvesting and processing costs for anchovy and $20 million for herring.

The additional value of precision management could exceed the costs of the northern anchovy fishery by $\$40\,000 \cdot \mathrm{yr}^{-1}$ or $\$0.10 \cdot \mathrm{t}^{-1}$ (this assumes an optimum fleet size and processing facilities, and annually adjusted quotas). If all clupeoids were managed this way, and the marginal biological yields were used for meal and oil, the restored 25 million t clupeoid yield would support $2.5 million from precision management. Thus, the long-term clupeoid yield would have a perpetual expected monetary value of the order of $250 million annually at 1978 costs and values. Development and implementation of precision management techniques would yield an additional $2.5 million annually with existing methods.

Bell et al. (1975) project a fivefold increase in price for fishmeal by the year 2000 (approximately 15 yr), and this they projected would accompany a decline in supply from a maximum of 30 million to 15 million t (Anonymous 1982). They also projected a conversion of products from the clupeoid stocks to maintain a level price-function for sardines while doubling the tonnage used to 2.5 million t. Even with the improvement in human fertility trends (Coale 1983), the human population will triple by the year 2100. Thus, we find that the expected monetary values of Huppert (1981) could be a moderate underestimate.

In summary, there has been a transition in research objectives for clupeoid fisheries in the past 30 yr from exploratory fishing to define new stocks to management research to restore depleted stocks and maintain the production of existing stocks. Increasingly realistic biological models of population growth combined with economic models of fishing efficiency and monetary value can assist us in establishing perspective on the perpetual values of existing uses of clupeoid stocks. The most expensive segments for management advice can probably be coupled for several species in the temperate and tropical areas to increase efficiency. The restored biological yield of clupeoids would approach 25 million t, and rise in prices for fish meal and the conversion of end products from clupeoid stocks from meal and oil to canned and cured products will tend to increase the expected monetary values. The projected yield of $2.5 million from precision management of the restored clupeoid stocks represents the costs and precision of methods as they existed in 1978. It would seem that reduction of costs of management advice is more urgent than increases in precision for sustained management of naturally variable clupeoid stocks.

Recruitment Prediction

Huppert et al. (1980a) evaluated recruitment assessment but did not involve prediction; thus, the economic value of recruitment prediction as a function of lead time and precision has not yet been explored. The values would appear to arise from planning alternate uses for fleet and processing plants during the inevitable closures. Other values might arise from early increases in quotas after the recovery of the stock and earlier closures following the projection of poor recruitment. The research objectives under this topic should involve cost and precision studies of new methods and the merger of recruitment prediction technology and tactics for several stocks in a region, and for the global adaptation of fundamental progress in recruitment studies.

Predictions of stock size in the clupeoids will have three characteristic elements: (1) the size of the spawning stock, (2) the locations, growth, and survival of the juveniles, and (3) the survival rate (R. D. Methot, pers. comm.) and the fecundity of adults. For the purposes of this paper, the sections to follow will emphasize direct measures of the O-group and environmental influences. The emphasis will be on the development and implementation of low-cost indices of recruitment in clupeoids.

Direct O-Group Studies

Current methods of study of the O-group clupeoid seem confined to labor and ship-time intensive direct sampling; the quality of the samples, in terms of representivity, precision, and accuracy, is in question. The strategy of conversion to lower cost methods rests heavily on the question of when the size of the incoming year-class is determined. It is also possible that the time of recruitment determination changes among years.

A new method for determining the location of juvenile anchovies and directing samples to determine growth and survival has been developed and tested (Hewitt et al. 1976; Holliday 1980). The method consists of three steps: (1) mapping schooled fish targets with conventional sonar, (2) estimating fish size with gas-bladder resonant return of broad-band sound, and (3) trawling to determine species composition. Discrimination of bladder-bearing fish from squid and pelagic crab aggregations is possible, and the length and age of anchovies can be evaluated to a 25-mm length category or 60-d age group for larval and juvenile anchovies between 10 and 110 mm in length. Adult anchovies can be discriminated from the juveniles and larvae, and these latter could be separated into late larvae (10–35 mm), early juveniles (35–60 mm), and late juveniles and prerecruits (60–85 and 85–110 mm, respectively). The precision of the measurements should be within the useful range because continuous line-transect surveys can be partitioned into independent estimates and weighted for representativeness. This method would probably detect recruitment failure and distinguish between moderate and exceptionally large year-classes. Such a method might also replace direct spawning biomass estimates in some years and furnish the continuity needed for management purposes in years when the biomass is too low or so high as not to require direct measures for setting quotas or closures.

Until one knows the success and dependability of the environmental indicators and predictors of recruitment discussed below, it will not be possible to define the direct O-group measurements necessary for perpetual management of clupeoids. It is likely, though, that the current status of O-group direct evaluation techniques will have to be improved to test and evaluate the environmental indices for long-term operational annual recruitment predictions. Thus, the development of direct measures of recruitment will accelerate the postulation (Bakun and Parrish 1982), evaluation (Parrish and MacCall 1978), and implementation of efficient environmental prediction of clupeoid recruitment.

Environmental Prediction of Recruitment

The eventual efficient predictors of recruitment will likely entail inexpensive observations taken at high frequency over vast areas for a multitude of purposes. For the purpose of predicting recruitment the generalized measurement will be evaluated for its effect on growth and survival mechanisms of several categories in the life cycle of clupeoids. Examples of key life cycle events are the successful transition from embryonic to first-feeding larvae (Lasker 1975), maintenance of the feeding larvae in food conditions leading to fast growth and proximity to the juvenile brood grounds (Hewitt and Methot 1982), conversion from carnivory to omnivory at 60 mm for northern anchovy (Methot 1981), and the achievement of maximum cohort biomass (point D in Fig. 3) all in the first year of life.

Clupeoid populations appear to occupy the habitat rather intensely (Ryther et al 1971; Murphy 1966; Lasker 1970; Hunter and Leong 1981; Smith and Eppley 1982; Cushing 1982); thus, measures of primary and secondary productivity could serve to evaluate the timing and intensity of spawning and subsequent survival of growth of the cohort. This approach could be extremely useful where several schooling coastal pelagic species occupy overlapping planktivorous niches. Virtually all the techniques discussed up to now were directed at fishery population management. New economies could be realized by merging measurements for the regulation of multispecies fisheries such as are commonly pursued for clupeoids, scombrids, carangids, and gadoids in the upwelling areas and continental boundary currents.

Environmental measurements may be obtained from standard survey cruises, platform-of-opportunity data, and coastal measures of temperature, salinity, chlorophyll, and sea level. Estimates of temperature and chlorophyll can now be made by satellite or airplane (Lasker et al. 1981; Pelaez and Guan 1982). Large area averages of turbulence, transport, and upwelling can now be obtained from meteorological data fields (Bakun and Parrish 1982). Coastal birds may be monitored for chick production, survival, and growth (Anderson et al, 1982; Tovar 1983) and marine mammals are often monitored (Anonymous 1977). The primary inhibition in the use of the above indicators is that they are more in the realm of individual, intensive, short-term research and they have not yet been forged into the system necessary for effectiveness as a perpetual management tool.

For schooling coastal, pelagic fishes, including the clupeoids, it can be foreseen that the estimation of small-scale spatial intensity of their food will be more important than measurements integrated through depth and space. Holliday (1980) described systems for evaluating forage using multifrequency ultrasound (megahertz), and mergers with pumps and nets are natural applications of this acoustic tool. As in the case of direct measurements of the O-group clupeoids, these techniques will be useful for defining the indicative or predictive indirect measures we need to evaluate plankton composition, spatial pattern and productivity as controls on clupeoid juvenile growth rate and survival and adult fecundity.

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